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THE CONSTRUCTION, VALIDATION, AND BEHAVIOR OF A POLLINATION AND FRUIT SET MODEL FOR 'DELICIOUS' APPLES

By

Gloria DeGrandi-Hoffman

A DISSERTATION

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

DOCTOR OF PHILOSOPHY

Department of Entomology

1983

ABSTRACT

THE CONSTRUCTION, VALIDATION, AND BEHAVIOR OF A POLLINATION AND FRUIT SET MODEL FOR 'DELICIOUS' APPLES

By

Gloria DeGrandi-Hoffman

A computer based, interactive, simulation model has been developed to predict pollination and fruit set in 'Delicious' apples. Predictions are based upon updates on the number of honey bees cross-pollinating apple blossoms, and the probabilities that blossoms in various age classes will set fruit if cross-pollinated. The rate of blossom aging is based on temperature, while the size of the cross-polinating honey bee population is a function of temperature, wind, solar radiation, honey bee population size, and stage of the apple bloom.

During the model's construction, field estimates on the size of the honey bee population carrying cross pollen were needed to validate this component of the program. Field data indicated that this population was of considerable size. Previously, pollen from unrelated apple varieties was thought to be transferred by honey bee movement from tree to tree due to competition for nectar. Our simulations predicted that competition for nectar could not create a cross-pollinating population as large as that found in the field, and that these bees were originating from another source. It has been concluded that honey bees were transferring compatible pollen in the hive through contact between nestmates. The model bases its predictions on the size of the pollinator population on both competition for nectar, and in-hive pollen transfer.

The pollination and fruit set model (REDAPOL) demonstrated that the strongest effects on fruit set were weather and the availability of compatible pollen. Weather infulenced both the intensity of honey bee foraging activity and the duration of 'Delicious' and pollinizer bloom. The latter affect the degree of bloom overlap and the number of open 'Delicious' and pollinizer blossoms at any given time. Blossom number affected the availability of compatible pollen, as did orchard design and the ratio of 'Delicious' fruit set under the widest range of weather conditons was predicted to occur in orchards with one-to-one ratios of 'Delicious' and pollinizer trees. The arrangement of trees did not strongly influence fruit set according the the model's predictions.

ACKNOWLEDGMENTS

The author wishes to express sincere appreciation to her advisor, Dr. Roger A. Hoopingarner for his invaluable assistance and support throughout this project. Special thanks are also extended to Mr. Ron Pulcer for contributing his talents and expertise in writing the computer program. Dr. Karen K. Baker is also gratefully acknowledged for her contributions in the electron microscopy sections of this thesis, and the advances in this work that can be attributed to her contribuiton.

The author would like to thank her committee members Drs. Stuart Gage, Mark E. Whalon, Martin J. Bukovac, and Frank G. Dennis for their valuable input and discussions. Appreciation is also extended to Mr. Ken Dimoff for his assistance in experimental design and data analysis, and Ms. Connie Crancer and Mr. Mke Dunlap for their excellent technical support. I also wish to express my graditude to Dr. James E. Bath (department chair) for his tremendous support of this project, and his advice and encouragement.

The author would also like to thank the growers who cooperated in this study. These include Jerry Stanek, James Embsen, Don and Kevin Herman, and John and Jeanne Ashby. I would also like to thank Dr. Stanley Flegler for his assistance in operating the scanning electron microscope, and Ms. Genevieve Macomber for technical assistance in the preparation of the photographic plates.

I am most grateful to my husband, Rich, for his moral support during this project and for his assistance in bringing this work to completion. I would also like to thank my family for their constant encouragement and support.

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GENERAL THESIS INTRODUCTION

Like many other biological processes, insect mediated pollination can be viewed as a system whose end product (fruit set) is a function of several components. Some of these include weather, flower attractiveness and reproductive state, and the size of the honey bee population capable of cross pollinating blossoms. By defining the relationships between these components and updating their values over time, it may be possible to predict fruit set rates under a broad range of circumstances. To test this, a pollination and fruit set model was proposed for 'Delicious' apples.

Because pollination and fruit set have never been examined using a systems approach, colony/hectare requirements for commercial fruit set in numerous crops have remained undefined. This information gap may indeed be partially responsible for the inconsistent set often associated with 'Delicious' apples. In the east and midwest 'Delicious' production is only about 40% of its potential, and in the midwest this represents an annual crop loss in excess of $85 million (Anonymous 1978). Still, if growers seek advice on the rate of colony introduction needed in their orchard to insure adequate cross pollination, the recommendations they receive will be based more on past experience than controlled experimental findings (McGregor 1976). In addition, recommendations for 'Delicious'-pollinizer tree arrangements in orchards, to insure sufficient compatible pollen also have not been adequately tested.

A pollination and fruit set model could generate recommendations for colony/hectare requirements, and predict maximum fruit set rates for various 'Delicious'-pollinizer tree arrangements. Colonies/hectare and arrangements of

'Delicious' and pollinizer trees could be simulated with the model, and potential fruit set predicted under various weather conditions. The model could also predict how long colonies would be needed in an orchard. This could be accomplished by setting a fruit set goal for a grower based upon blossom density. The goal would be expressed as the ideal percentage of blossoms needed to develop into fruit for a commercial set to be achieved. Because the model would deliver daily fruit set predicitions, it could alert the grower when during the period bloom a fruit set goal had been achieved, so that colonies could be removed and oversetting could be prevented. The model could also be programmed to predict potential fruit set 48 hours into the future (based on input weather predictions) and report to the grower if a particular fruit set goal could be achieved with the number of colonies that have been introduced.

In addition to agricultural applications, pollination and fruit set models could be used to study the interactions of honey bees and flowering plants. Currently, the mechanism by which honey bees acquire a second apple variety's pollen, when their foraging area is often a single tree, is not well understood. Although movement of honey bees between trees has been used to explain fruit set in self-incompatible sterile varieties (Butler 1944, Free 1962, Free 1966, McGregor 1976), it does not account for oversets on self-incompatible trees planted in solid blocks or at remote locations from a compatible pollen source. During the development and validation of this model, defining the source of honey bees carrying compatible pollen was a critical factor in predicting the rate of fruit set.

In the model, fruit set predictions were essentially a combination of updates on the size of the honey bee population capable of cross-pollinating blossoms (pollinators), and the probabilities of fruit set in blossoms whose age had also been updated. Currently information on changes in fruiting potential with regard to weather, blossom age, and state of bloom is limited, but does indicate a trend where a blossom's fruit set potential declines with time. By combining updated estimates on blossom fruit set probabilities with numbers of cross-pollinations, approximations could be made on the number of fruit that had been set at any time in bloom.

Ultimately, pollination and fruit set models may afford a "total picture" perspective on the relationship between honey bees and flowering plants. With the model, various orchard designs subjected to different weather conditions and colony densities could be simulated and evaluated for their fruit set potentials. This information could generate recommendations for 'Delicious'-pollinizer arrangements that would enhance the colonies' cross-pollinating potential, and produce colony/hectare recommendations that would be specific for the year and orchard site.

Before a pollination model could be built, the source of honey bees in a cross-pollinating state (pollinators) had to be defined. Because the model would have to generate predictions on the size of this population before fruit set predictions could be made, defining the source of pollinators had to be viewed as a pivotal point in the model's construction. A systems approach in conjuction with field experiments was used to define the pollinator population. The sequence of events leading to the acquisition of compatible pollen can be simulated, and through sampling, the field population's size could be estimated. By synthesizing this information, an explanation on the source of pollinators could possibly be obtained, which would afford new possibilities for the management of pollination and fruit set.

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LITERATURE REVIEW

Although 'Delicious' is America's number one apple variety, it is also the most inconsistant producer especially in the east and midwest (Howlett 1928, Roberts 1947, Gardner et al 1949). Delicious is a totally self-sterile variety and requires unrelated cultivars (pollinizers) to be planted nearby to serve as a compatible pollen source. Insects, particularly honey bees, are necessary for the transfer of pollen from the pollinizers to 'Delicious' trees (Roberts 1945a, Free 1960, McGregor 1976).

As a variety 'Delicious' has numerous problems that all undoubtedly contribute to its erratic fruit set. 'Delicious' flower buds are also less resistant to low temperatures than other varieties, both before and during bloom (Hartman and Howlett 1954). Compared to other varieties 'Delicious' exhibits exceptionally strong apical dominance, so that fruit set on lateral spurs is significantly depressed by the presence of fruit on the terminals (Howlett 1928). Detjen (1929) stated that the terminal flower on a cluster base was "better constituted and better situated" and usually gave a higher percent set over the laterals. In 'Delicious' the positioning of lateral flowers also affects their quality. Laterals that are not situated in the axil of a leaf do not set as well as those lateral flowers with subtending leaves (Howlett 1932).

Although 'Delicious' ovaries (and most other apple varieties) have the potential to set 10 seeds, it is not unusual for these blossoms to open with less than a full complement of ovules. Hough (1947) stated that in the development of 'Delicious' ovules, the most frequent abnormality was either tardy initiation of the megaspore mother cell, or a slower development rate of megaspores and embryo sacs. Such retarded embryo sacs are seldom expected to develop fully in time for fertilization. Other apparently normal embryo sacs degenerate soon after anthesis, significantly shortening the effective pollination period for the variety. Hartman and Howlett (1954) stated that delayed development and early degeneration of the embryo sac nuclei at and subsequent to anthesis has a genetic basis in the variety.

In addition to the loss of fruiting potential from ovule degeneration, Hartman and Howlett (1954) found that fertilization was greatly decreased when pollination was delayed for 48 hours after anthesis. The reduction in fruiting potential was attributed largely to a loss of stigma receptivity. Another fruit set constraint in 'Delicious' is related to the time during bloom when a particular blossom opens, which seems to influence its probability of setting fruit if cross-pollinated. Lapins and Arndt (1974) reported that during cool weather 'Delicious' blossoms pollinated the first few days of bloom set fruit while those pollinated later did not.

The morphology of 'Delicious' blossoms may further reduce their chances of setting fruit, because honey bees can remove nectar without contacting the stigma. Consequently, these foragers often do not cross-pollinate blossoms. This occurs because 'Delicious' blossoms are characterized by short pistils and upright staminal filaments, which allows bees to extract nectar without touching the stigma in a majority of cases (Roberts 1945a,b. Robinson 1979). In addition, gaps exist at the bases of the staminal filaments around the nectaries. This allows honey bees to stand on the petals and extract nectar without contacting the stigma. Only 'Northern Spy' has basal gaps comparable to 'Delicious', and has a higher percentage of bees visiting blossoms without touching the stigma

(Robinson 1979). In light of this information the importance of basal gaps on fruit set is questionable, since 'Northern Spy' does not have fruit set problems.

Weather is the common denominator between flowering plants and their pollinators, because the effects on one are invariably felt by the other. Pollinator activity can be directly affected by weather conditions, or indirectly by their influence on the crop (Ribbands 1953 cited by Williams and Sims 1977). Insect flight, flower quality and attractiveness are all affected by temperature, wind, relative humidity, and solar radiation.

Lundie (1925) reported that the threshold temperature for honey bee flight varied with the time of year and weather conditions. In April the threshold temperature ranged between 12° and 14°C, while in May it rose to 16° to 18°C. On cloudy days the threshold was 2° higher. After a certain threshold temperature is achieved, flight activity is further influenced by light intensity. Under normal conditions optimum temperatures occur later in the day than optimum light, but morning bee counts regularly give higher numbers than afternoon counts at the same temperature. This is caused by the higher light values that exist in the morning hours. Light intensity, especially in the ultraviolet range, declines rapidly in the afternoon, and although temperature may remain stationary or even rise, bee counts gradually recede with fading light (Brittain 1933, Szabo 1980).

The foraging population is also affected by wind speed. Because honey bees fly at speeds of about 6.3 m/sec, it is reasonable to assume that wind speeds greater than or equal to that average affect foraging activity (Williams and Sims 1977). Rashad (1957) found that wind speeds of 4.9 m/sec reduced pollen gathering activity, and at winds greater than 9.4 m/sec honey bees stayed in the hive. Pollinator activity on apple blossoms was greatest at wind speeds of .44 m/sec (1 mph), but steadily decreased to 1/7 that number at speeds of 3.1 m/sec (Brittain 1933 cited by Free 1960). From these data it was concluded that even light winds affect the size of the foraging population.

Aside from effects on honey bee foraging, weather also influences the attractiveness and quality of apple blossoms. The duration of the apple bloom is apparently temperature dependent. When the weather is warm, bloom will last for about five to seven days while cooler temperatures can prolong bloom to almost two weeks. Individual flowers will not open if temperatures are below 10°C (Free 1960, McGregor 1976). Because apple blossoms are dish-shaped and have exposed nectaries, their attractiveness (in terms of caloric reward to a forager) can also be strongly influenced by weather. Rain or dew dilutes nectar making blossoms less attractive to nectar foragers. High temperatures and wind concentrate the nectar and allow blossoms to regain their attractiveness (Butler 1944, Roberts 1945a).

Weather can also effect the chances that a cross-pollination will cause fertilization and fruit set. Pollen germination and pollen tube growth are both temperature dependent, and low temperatures can prevent fertilization even if adequate masses of pollen are placed on the stigma (Martin 1972). In addition, slow pollen tube growth has a compounding affect in reducing fruit set, because the stigma and ovules continue degenerating while the pollen tube is growing (Hartman and Howlett 1954).

Because 'Delicious' is self-incompatible, unrelated apple varieties (pollinizers) must be planted nearby to act as a compatible pollen source . Some varieties are better pollinizers than others because they possess certain characteristics. For instance, ideal pollinizers flower annually and bloom two or three days before the 'Delicious' blossoms open. The pollinizer should also produce large amounts of viable and compatible pollen (i.e. the pollinizer must be a diploid variety) and remain attractive for the duration of the 'Delicious' bloom. Recommendations for the best pollinizer varieties are area dependent because a pollinizer that may have an overlapping bloom with 'Delicious' in one region may not in another (Dennis 1979). For example 'Northern Spy' and 'Golden Delicious' are listed by Roberts (1947) as being excellent pollinizers for 'Delicious', but in Michigan both varieties flower after 'Delicious's king blossoms have lost their attractiveness and probably their receptivity. Based upon yields of 'Delicious', 'Rome Beauty,' 'Northwestern Greening,' 'Wealthy,' 'Jonathan,' 'Golden Delicious' and 'Northern Spy' are reported to be the best pollinizers in various sections of the U. S. (Roberts 1947). In Michigan 'Jonathan' is considered the best 'Delicious' pollinizer (Anonymous 1978), although 'McIntosh', 'Empire', and 'Golden Delicious' are also used.

In addition to environmental and genetic factors limiting fruit set, honey bee behavior also exerts a strong influence. Honey bees choose to forage a crop for nectar because it consistently gives a caloric return greater than that expended in the reward's search and extraction (Heinrich and Raven 1972). In the case of apple, a large tree with heavy flowering will prompt individual honey bees to restrict their foraging areas to a single tree, and continue to visit it on successive trips (Butler 1944, MacDaniels 1931, Roberts 1956). In an orchard of standard trees, at best, honey bees will visit an average of two trees per foraging trip (Free 1966). In dwarf tree hedge row arrangements, honey bees have been found to work along a hedge row, and probably restrict their foraging areas to about 3m sections of a row during one trip. Nearly all honey bees that do move to other rows move to an adjacent row, which possibly explains why more fruit is sometimes set on trees next to the pollinizer rows (Williams 1959, Free and Spencer-Booth 1964b). Honey bees also appear to discriminate between varieties, and exhibit cultivar fidelity (Free 1966). Because of these foraging behaviors, it is recommended that to insure maximum pollination, pollinizer varieties should be planted as every fifth tree in rows of main variety trees (Free and Spencer- Booth 1964a).

Although a majority of honey bees appear to have established foraging areas, superimposed upon this population is another of wandering bees which may be responsible for cross-pollination in orchards (Butler 1944, McGregor 1976). Wanderers have no set foraging areas, and can work several trees on the same trip from the hive. This wandering population could be the result of competition for nectar which causes bees to drift from one area to another. Young bees which have not yet acquired definite habits or foraging areas could also contribute to this population (Butler 1944).

Although honey bees have been observed to move from tree to tree, pollinators that arise from this situation may be only part of the total pollinating population. In 1954, Karmo and Vickery speculated that honey bees could possibly pick up pollen in the hive from contact with nest mates, and hence carry pollen on their bodies from species or varieties that they never visited. This source of cross pollinators could explain why isolated self-incompatible trees set fruit. Other investigators have also found that honey bees carry viable pollen from several plant species from one foraging trip to the next (Kendall 1973). Additional investigations showed the viability of insect-borne fruit pollen was usually similar to that of pollen from blossoms taken from the orchard in which the insects were collected (Kendall 1973, Kendall and Solomen 1973). From this information, it is apparent that individual honey bees may be leaving the hive carrying pollen from flowers that they never visited.

Whether or not inconsistent set in 'Delicious' is pollination related is still open to speculation. When the weather before, during, and immediately after bloom is favorable, 'Delicious' set is so heavy it needs to be thinned. Only 5-10% of the blossoms are required to develop into fruit for a full commercial set, but the chances of fruit set occurring are best early in the bloom period. Consequently, a good commercial set should result if ovules are viable and flight weather is favorable at this time.

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DATA COMPILATION LEADING TO THE DEVELOPMENT OF A POLLINATION AND FRUIT SET MODEL FOR 'DELICIOUS'

INTRODUCTION

The rate of fruit set in an apple orchard is a variable whose value depends upon weather, orchard design, flower quality and pollinator population size. If accurate fruit set predictions are to be made, they must incorporate these factors and their changing influence on the fruit set rate over time. A systems science approach could be used to estimate the rate of fruit set because it permits both flexibility in analysis of various orchard designs, and the ability to update fruit set rates as the bloom and foraging population change. With this in mind, a simulation model for 'Delicious' apple was constructed to predict pollination and fruit set during the bloom period. The model's predictions are based upon the specific orchard parameters input by the grower, and weather conditions existing during bloom.

The essence of the model's fruit set predictions is the ability to update the fruit set rate as weather conditions change during bloom. All the parameters that affect the rate of fruit set including the number of open blossoms, attractiveness and quality of blossoms, size of the foraging population (after the number of colonies introduced per acre has been considered), and the probability that cross-pollination will lead to fruit set are tied to weather conditions. Significant honey bee flight occurs only if days are warm, sunny, and calm. Nectar secretion and sugar concentration, which dictate blossom attractiveness, are also weather dependent. Finally, temperature influences the fruit set potential of blossoms in terms of their stigma receptivity, rate of pollen tube growth, and ovule receptivity. These factors ultimately effect the probability of cross pollination leading to fertilization and fruit set.

During the model's construction, predictions on the source and size of the pollinator population (i.e. honey bees working 'Delicious' blossoms while carrying compatible pollinizer pollen on their bodies) were seen to be a pivotal point on which fruit set predictions could be made. The origin of this population has never been definitively described. Several authors have reported that pollinators could arise from competition for nectar on the pollinizer, which would prompt foragers to wander between trees and hence cross pollinate blossoms (Butler 1944, Free 1962, Free 1966, McGregor 1976). Another source of pollinators was reported by Karmo and Vickery in 1954. These investigators speculated that pollen collected during the day could be transferred among nest mates through contact in the hive. Consequently, honey bees could be leaving the hive carrying pollen from plant species that they had never visited. Although it is logical to assume that both sources of pollen transfer exist, their contribution to the pollinator population size under different weather and orchard conditions has never been investigated. During the construction and validation of this model, it was possible to better define this population, and how it changes with orchard and weather conditions.

MATERIALS AND METHODS

General Features of the Model's Development

The model's program was written in Fortran-IV and input on a CDC series 170 model Cyber 750. The model is programmed to use weather data (temperature, wind speed, solar radiation, and relative humidity) collected by a Campbell Scientific CR-21 micrologger.* Various field experiments were conducted in two sites in 1981 and 1982. In 1981 the Michigan State University Horticulture Farm (located in East Lansing, Ingham County) and Stanek and Sons' Orchard in Traverse City (Leelanau County) were used. In 1982 the same sites were used again and in addition Herman's Orchards of Sutton's Bay (Leelanau County) and John and Jeanne Ashby's Orchards in Jonesville. These sites were chosen for their orchard design and geographical significance.

In 1981 temperature was recorded on a hygrothermograph in both sites. In 1982 temperature was again recorded on a hygrothermagraph, but at Stanek and Sons' orchard a Campbell Instrument CR-21 Micrologger was used. Temperature, wind, relative humidity, and solar radiation were recorded using this instrument.

Predicting Blossom Density Per Tree

In 1982 groups of 'Delicious' (at Stanek and Sons' and Ashby's orchards), 'Empire' (at Ashby's only) and 'McIntosh' (at Stanek and Sons only) trees were chosen after stratifying the orchards into 3 sections. Tree height and width were measured, and the distance between the ground and first main branch recorded. Flowering spurs were counted on meter long branch sections, and average spurs per meter was calculated. Finally the flowering spurs on the entire tree were counted. The data from these trees was also used in experiments to test the effects of floral density on fruit set.

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* Campbell Scientific Inc., P.O. Box 551, Logan, Utah 84321

Defining Bloom Curves for 'Delicious' and 'McIntosh' Varieties

In 1981 and 1982 open blossoms on 'Delicious' and 'McIntosh' trees (at the MSU Horticulture Farm and Stanek and Sons' Orchards) were counted daily on 1m branch sections beginning on the first day of bloom. Daily flower counts were taken only at the Horticulture Farm in 1982. Counts were made from the same branches throughout the blooming period. Four counts were taken per tree, one count from each side.

Nectar Secretion and Replacement

Nectar samples were taken from blossoms on their day of anthesis in 1981 at both orchard sites. Blossoms were enclosed in nylon mesh bags while in the 'balloon stage' to protect against nectar removal by foragers. Samples then were taken by placing a Drummond microcap (one-microliter size) between the staminal filaments and dabbing the nectary tissue. In experiments to determine nectar replacement rates blossoms were sampled, then depetaled to decrease their chances of being foraged during the sampling interval. Nectar volume was calculated by measuring the amount of nectar within the tube to the nearest millimeter, and then converting this to microliters.

Measurements of Flight Activity Using Erickson-Waller Traps

At the MSU Horticulture Farm in 1981 the entrances of two colonies were equipped with Erickson-Waller traps to measure foraging activities (Erickson et al. 1975). Hourly pollen samples were taken from these traps and frozen (separately) for later analysis. Relative flight activity and percentage of pollen collectors (i.e. honey bees with pollen loads in their corbiculae) in the foraging population were also recorded hourly using these traps.

Pollen Analysis Using Light Microscopy

One gram samples of pollen collected in Erickson-Waller traps were acetolyzed (according to the procedure of Faegri and Iversen (1964)) and stained with 1 ml of 0.01% solution of methylene blue* (to facilitate identification). Pollen was identified as being either apple or non-apple using light microscopy. Calculations on the percentage of apple pollen in the sample were made using a Lovins micro-slide field finder, and counting apple and non-apple pollen grains in 30 fields.

Sampling for Cross Pollen on Honey Bees and Apple Stigmata

In 1982 at the MSU Horticulture Farm and Stanek and Sons' Orchards honey bees working apple trees and competitive plants were sampled periodically during the day. Honey bees were removed from the flowers they were foraging, put in individual vials, and frozen. The pollen on the body of these insects would later be removed and examined using scanning electron microscopy (SEM).

In 1982 'Delicious' and 'McIntosh' blossom stigmata were removed at the end of the flight day from all orchard locations, except Herman's and Ashby's. Samples were kept frozen until examined for cross-pollen using SEM. Finally, pollen samples were taken from apple varieties and competitive plants that were in bloom with the 'Delicious' and 'McIntosh' trees. These samples would be used for comparisons with pollens found on honey bee bodies, and apple stigmata.

Honey Bee Foraging Activity on Trees

At the MSU Horticulture Farm in 1981 and 1982 honey bees were counted hourly on 8 'Delicious' (Millerspur sport) and 8 'McIntosh' (Macspur) trees. Because standard sized trees were used, honey bee counts were made simul-

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*Methylene blue, C. I. 52015, 91% dye content taneously by two observers stationed on either side of the tree. Each observer counted the honey bees seen on their half of the tree during a 45 second interval.

At Stanek and Sons' orchards semi-dwarf 'Delicious' (Red-Chief) and 'McIntosh' (Macspur) trees were used for hourly honey bee counts. Because these trees were small, all the honey bees on a tree (seen in a 45 second interval) were counted by one observer. Eight trees were used in each hourly sample.

SEM Analysis of Pollens on Honey Bees and Floral Stigmata

Body pollen of frozen honey bee samples was removed by rolling the insect's body over an aluminum SEM stub coated with adhesive. The sample was sputter-coated with gold for three minutes. Non-germinated pollen grains were identified as self-, cross-, or non-apple pollen using a JEOL JSM-35C scanning electron microscope operated at 15kV. This method of identifying varieties of fruit pollen using SEM was first reported by Fogel (1977 a,b).

Floral stigmata were prepared for SEM examination by placing them on an aluminum stub pretreated with an adhesive. The stigmata were then sputter coated with gold for 3 minutes and examined for self-,cross-, and non-apple pollens.

Relationship Between Flower Density and Final Fruit Set

In 1981 monthly fruit counts were conducted on branches of 'McIntosh' trees (at the MSU Horticulture Farm) used earlier to derive the flowering curves for this variety. 'Delicious' trees at the MSU Horticulture Farm with sparse flowering were also used in the experiment. All the flowers on these 'Delicious' trees were counted, and the resulting fruit recorded monthly.

In 1982 trees used to predict blossom density (from various tree parameters) were also used to monitor the percentage of blossoms setting fruit.

During bloom, flowering spurs on the entire tree were counted at the Traverse City and Jonesville sites. Monthly fruit counts were then made until harvest.

Effect of Distance from the Pollinizer on Fruit Set

In 1982 at the Sutton's Bay Orchard site 1m branch sections on four sides of 'Delicious' and 'McIntosh' trees were chosen for evaluation of fruit set. In this experiment, trees various distances from the pollinizer were selected. Monthly fruit set counts were performed at the site until harvest.

Seed Number in Retained and Abscissed Fruit

In 1982, seed counts were made on fruit retained on the tree and those abscised during 'June drop' at all orchard sites. Fruit was chosen at random from 'Delicious', 'McIntosh', and 'Empire' (at Ashby's and MSU Horticulture Farm only) trees throughout the orchard. Abscised fruit under the trees was also sampled.

RESULTS

General Flow Diagram of the Model and Explanation of Subroutines

The flow diagram indicating the subroutine sequence is diagrammed in Figure 1. The first subroutine called in the main program is "Initial" (Figure 2). In this subroutine all values for variables and arrays are set for the beginning of the simulation. Before leaving the subroutine, blossom age is updated and matricies containing rates of nectar replacement and probability of fertilization leading to fruit (based on the number of receptive ovules) are generated, for each age class of apple blossom.

The interactive portion of the simulation begins within the "Orchard" subroutine. The user is asked to provide details about the orchard's acreage, 'Delicious'-pollinizer block planting pattern, tree characteristics and spacing,

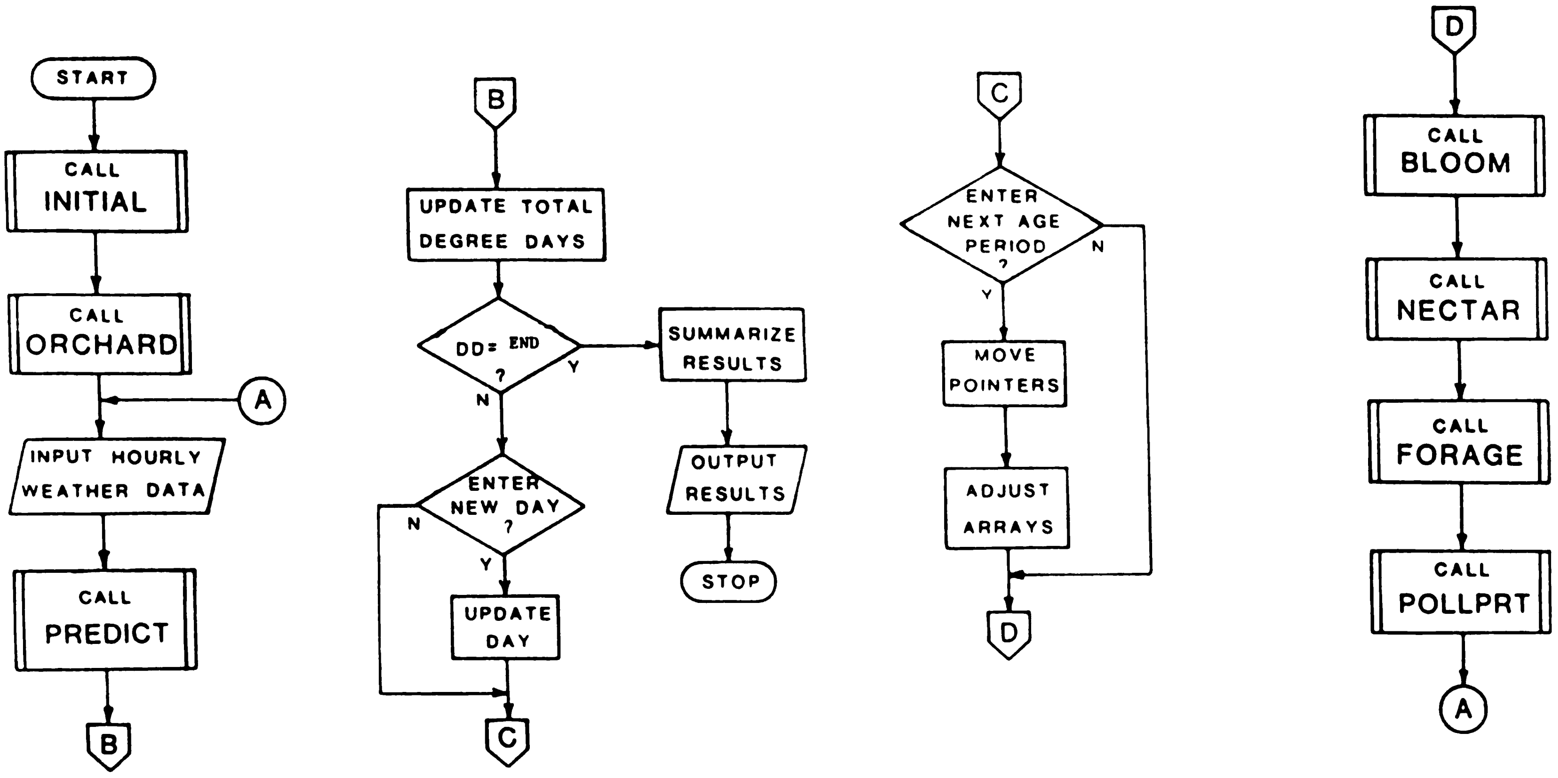


Figure 1. The sequences of subroutines comprising the pollination and fruit set program.

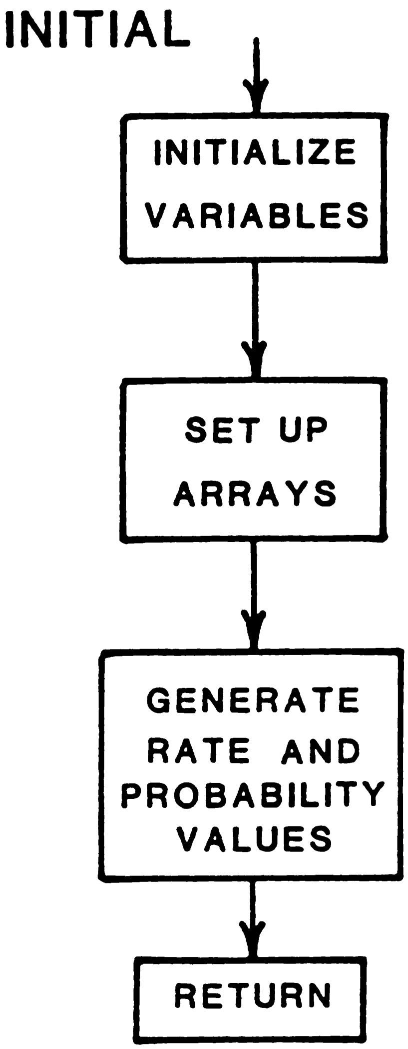


Figure 2. Sequence of operation in the "Initial" subroutine.

blossom counts and viability, and numbers of introduced honey bee colonies. From this data the subroutine calculates orchard parameters that will influence the rate of cross pollination and the number of available blossoms. With the exception of additional input of honey bee colonies, this subroutine is called only once during a run of the program.

Hourly weather data is next entered into the program from data collected on a Campbell Instrument CR-21 micrologger. Calculations on the number of open blossoms, their nectar content and viability, and the size of the foraging population are all weather based. For this reason, weather must be input before predictions can be made.

If a grower chooses to see predictions on future fruit set (24-48 hours into the future) with the current number of colonies per acre, the program will enter the "Predict" subroutine (Figure 3). Possible fruit set over a 24-48 hour interval is reported to the grower using weather predictions based upon daily high and low temperature, wind velocity, and probability of precipitation. The grower is warned that these are only predictions, not actual occurrences, and fruit set predictions are only as accurate as the input weather predictions.

After the program passes through the "Predict" subroutine, the next step is to update the time elements. The model runs on two distinct time units, chronological and physiological, both of which are stepped through simultaneously. Components that run on chronological time are weather, bee flight activity, and fruit set reports. They are updated hourly. The state of the bloom, and age of the flowers are described in physiological time (accumulated degree days).

After time is updated, the "Bloom" subroutine is called. "Bloom" is called once each hour, and updates the number of newly opened blossoms based on

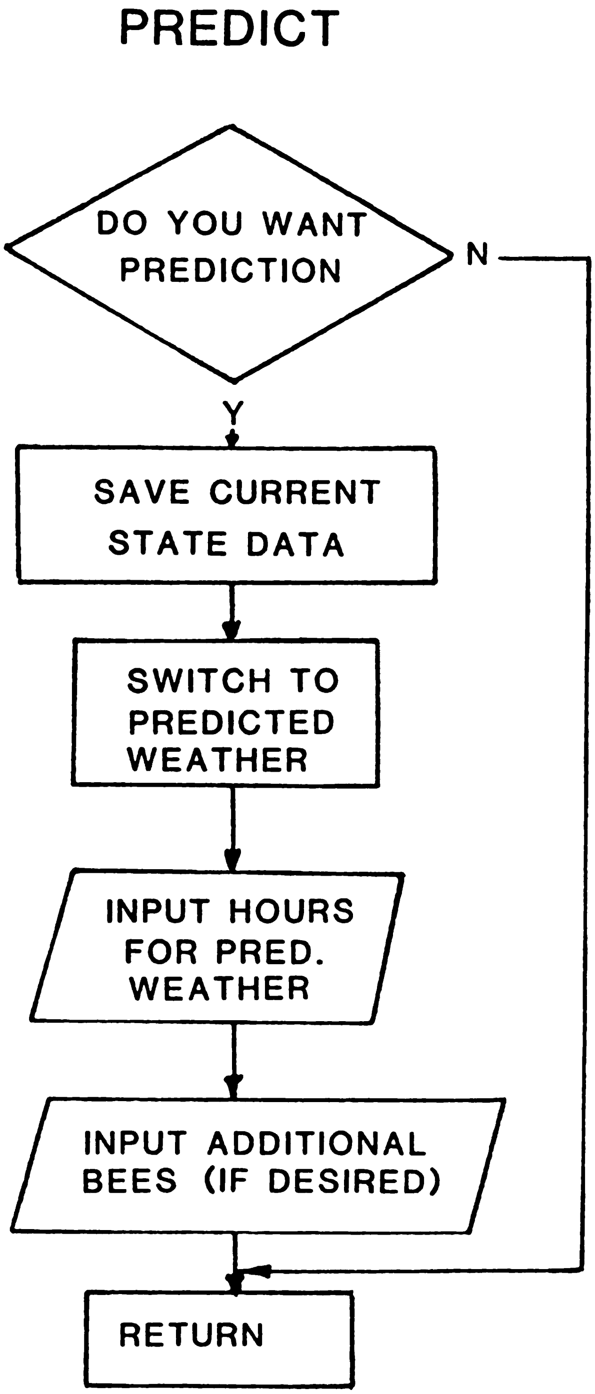


Figure 3. Sequence of operation in the "Predict" subroutine.

accumulated heat units. New flowers are placed in appropriate positions within an array named 'Full'. 'Full' contains only those flowers which currently contain a nectar load, and are attractive to honey bees. Another array called 'Empty' is the counter part to 'Full.' 'Empty' contains all flowers which currently have been visited that hour, and are unattractive to honey bees. The values in 'Full' and 'Empty' always sum to the total number of blossoms open that hour.

Following the update of flower number, the "Nectar" subroutine is called (Figure 4). This subroutine is called hourly to monitor the secretion of nectar in 'Delicious' and pollinizer blossoms. "Nectar" updates the total amount of available nectar in blossoms of each accumulated degree day age class. A honey bee visit or rainfall greater than .254cm during any hour is assumed to remove all nectar from the blossoms. Nectar is replaced after a bee visit or rain storm based upon the age class of the flower (as calculated in the "Initial" subroutine), and the hour's weather conditions (Figure 4).

Once the amount of nectar within a class of empty flowers is replenished to the attractiveness level, the blossoms are removed from the 'Empty' array and returned to the 'Full' array. This subroutine is called once each hour. It is assumed that blossoms open with a full complement of nectar.

After blossom number and attractiveness are updated, the size of the foraging population on apple is calculated in the "Forage" subroutine (Figure 5). This subroutine is called hourly, but will return to the main program if proper honey bee flight conditions are not met. Factors used to calculate the percent of the foraging force leaving the hive each hour include temperature, wind, solar radiation, and rain less than .127cm/hr. After the foraging population is calculated, a portion of it is lost to competitive plants based on the state of the

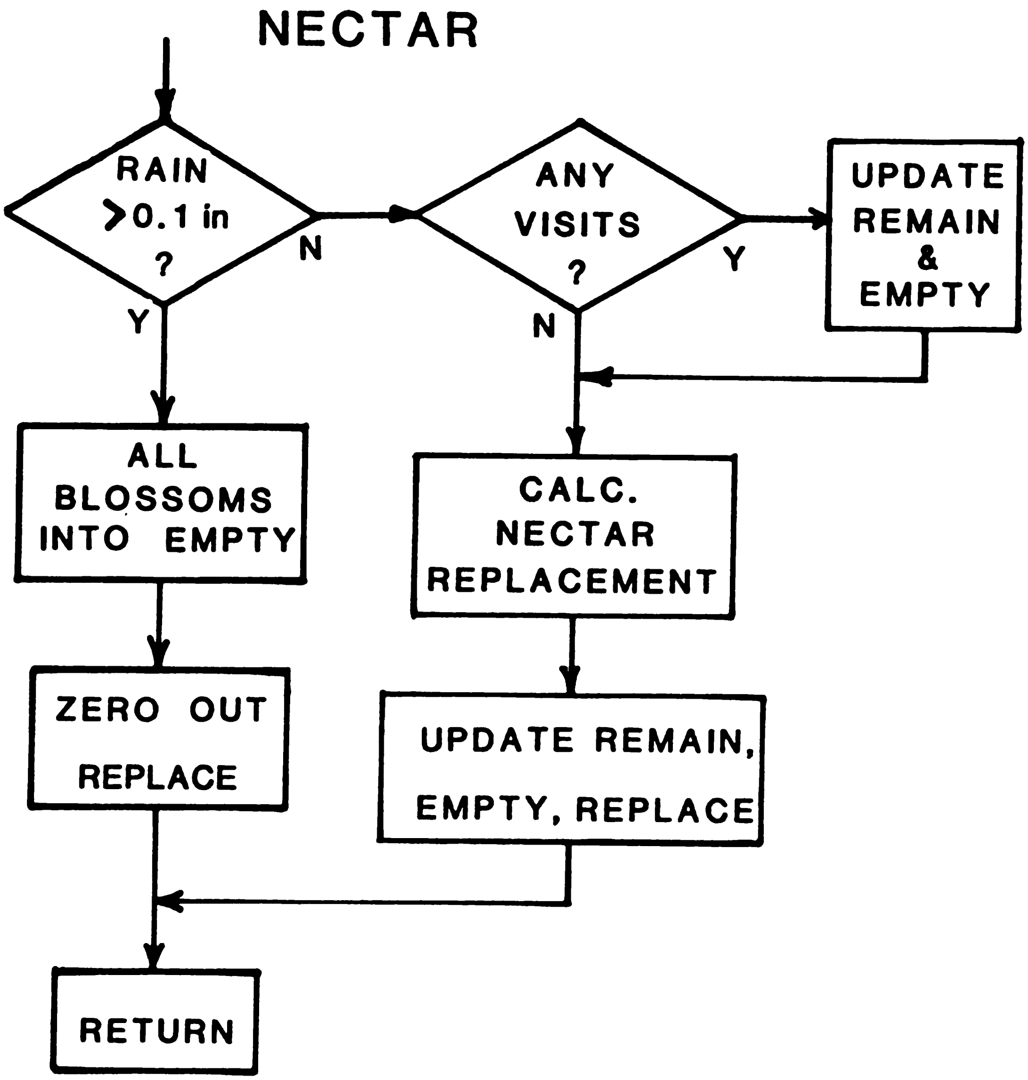
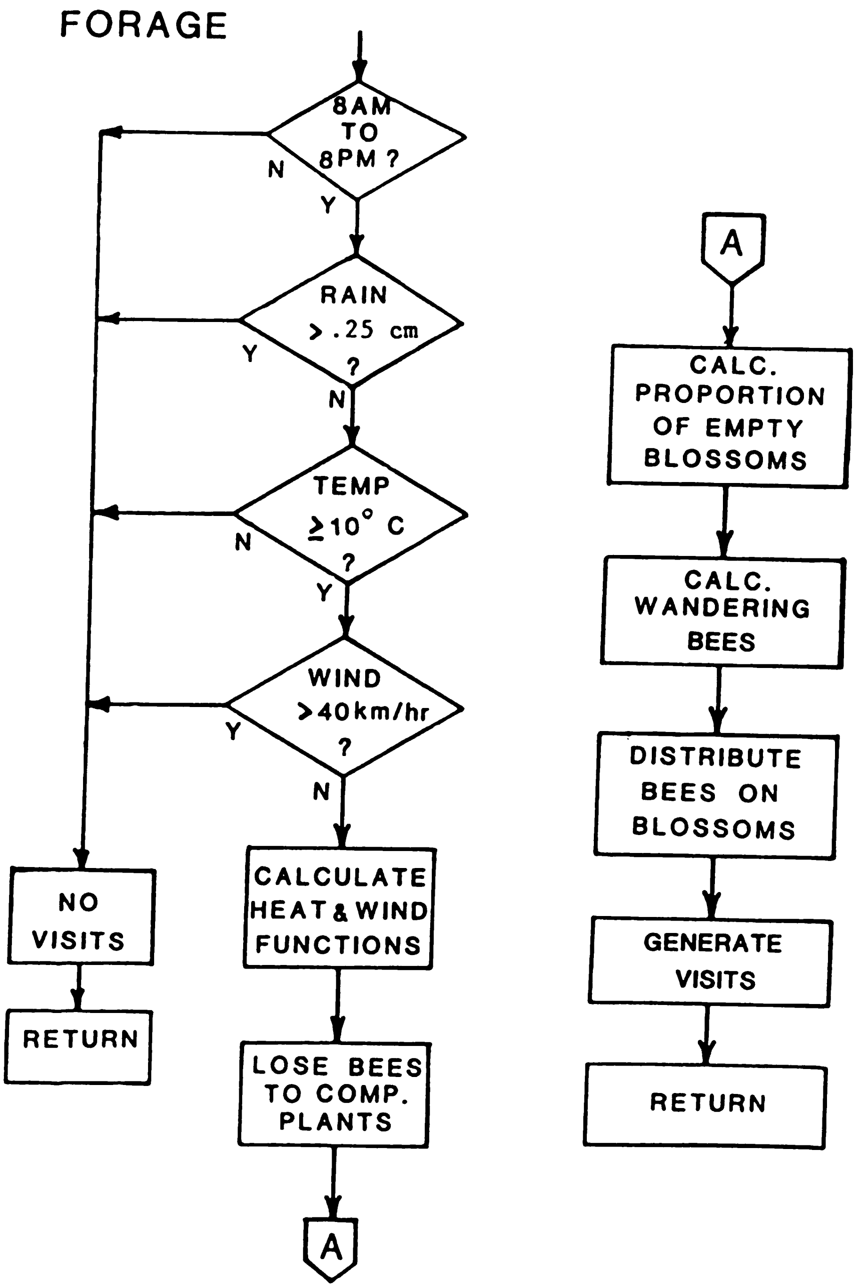


Figure 4. Sequence of operations in the "Nectar" subroutine.

Figure 5. Sequence of operations in the "Forage" subroutine.


FORAGE
8AM TO 8PM ?
N
Y
RAIN > .25 cm ?
Y
N
TEMP ≥10° C ?
N
Y
WIND >40km/hr ?
Y
N
NO VISITS
RETURN
CALCULATE HEAT & WIND FUNCTIONS
LOSE BEES TO COMP. PLANTS
A
A
CALC. PROPORTION OF EMPTY BLOSSOMS
CALC. WANDERING BEES
DISTRIBUTE BEES ON BLOSSOMS
GENERATE VISITS
RETURN

apple bloom. Competition for nectar among the honey bees on apple is calculated next, using the ratio of blossoms in the 'Full' array to those in 'Empty'. It is assumed that the portion of apple foragers finding five empty blossoms in a row will leave the tree. This population is referred to as "wandering bees." The "Forage" subroutine distributes the foraging and wandering bee population on to available blossoms, and generates the number of blossoms which have been visited in each age class. This information is then placed in the 'Visit' array, and control is returned to the main program.

Just as the foraging and wandering population size is updated hourly, so is blossom quality in terms of the probability of fruit set (if cross pollinated). Ovules are predicted to degenerate as the blossoms age (as a function of accumulated degree days), while the number of receptive ovules on the day of anthesis is predicted to be a function of the period of opening during bloom. King blossoms are predicted to open with a full complement of ovules and a .999 probability of setting fruit if cross pollinated on their day of anthesis. As the bloom ages, the probability of setting fruit on the day of anthesis decreases, so that the fruit set rate is greatest during the first few days of bloom. Because there is no data on ovule degeneration based upon accumulated degree days, the actual probabilities of cross pollination leading to fruit set at various blossom ages and period of anthesis has not been "hard coded" in the model. Currently different probabilities are being tested through model simulations to find which numbers result in the most realistic fruit set predictions.

The final subroutine called in the program is "Pollprt" (Figure 6). This subroutine integrates the values in the 'Visit' array, the number of wandering bees, details of the orchard, and values for ovule receptivity by age class

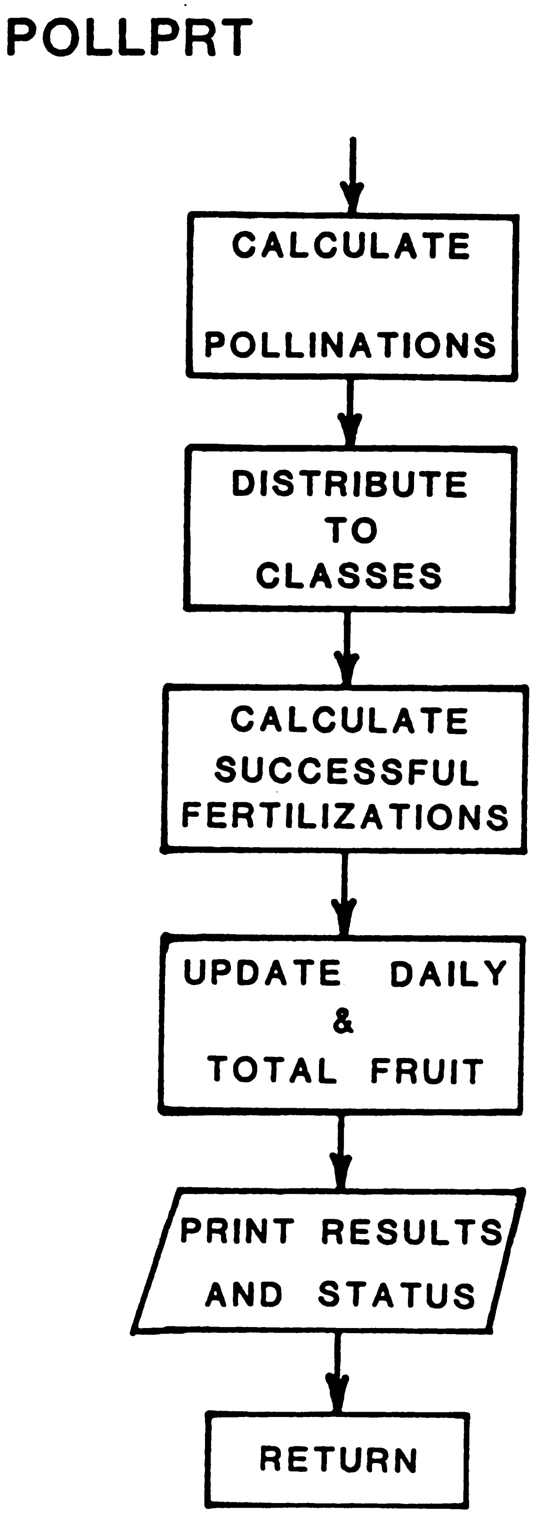


Figure 6. Sequence of operations in the "Pollprt" subroutine.

established in the "Initial" subroutine. By multiplying predictions on the number of blossoms cross-pollinated per hour (by age class) by their probabilities of fruit set, "Pollprt" calculates the number of cross pollinations which have resulted in fruit set. This subroutine is called hourly when honey bee flight is occurring. "Pollprt" updates the daily fruit set totals, and reports to the grower total fruit set which has occurred since the simulation began.

Calculating Blossom Number per Tree

In the programs first subroutine ("Initial"), the number of blossoms that will open during bloom is calculated from user input of various tree parameters. These include tree height, width, trunk height from the ground to the first limb of fruiting wood, and average number of flowering spurs (or flower clusters) per meter of branch. In the original program, the flowering part of a tree was equated to a sphere whose radius was one half the tree height minus the portion that was trunk. This information was then used to calculate the volume of a sphere using the equation: sphere volume = 4/3 $(\text{radius})^3$. It was then assumed that only two-thirds of the sphere volume was fruiting wood. The number of blossom clusters per tree was then approximated by multiplying the estimated volume of fruiting wood by the average number of flowering spurs per meter of branch. The number of blossoms per tree was then calculated by multiplying the estimate of blossom clusters per tree by 6 (McGregor 1976). Unfortunately when this method was tested against actual tree parameters, predictions of blossom clusters per tree were not good even after varying blossoms per spur and the percentage of the tree's volume that was flowering wood.

In 1982 at Stanek and Sons' and Ashby's Orchards 28 trees were selected and their height, width, trunk height, average number of flowering spurs/meter of branch, and the number of flowering spurs on the entire tree were measured. A multiple regression was performed regressing tree height, width, trunk height, and average number of spurs/meter of branch on total flowering spurs per tree. These parameters were found to be highly correlated to the number of spurs on the entire tree with the regression equation: (Total number of flowering spurs = 4.68 (Average spurs/meter of branch) + 36.6 (tree height) +106.0 (tree width) - 398.0 (trunk height) having a correlation coefficient of .975. The total number of spurs/tree was then multiplied by 5.5 to calculate the total number of blossoms per tree.

Although the regression equation had a high correlation coefficient, and is currently being used in the model, how well it actually predicts the total number of spurs/tree will need at least another year's data for validation. The 5.5 blossoms/spur is also an assumption based upon field observation while taking blossom counts, and could also have its accuracy increased through additional measurements.

Predicting the Progression of Bloom Using Accumulated Degree Days

Data from 'Delicious' and 'McIntosh' blossom counts taken in 1981 at the MSU Horticulture Farm and Stanek and Son's Orchard are plotted on accumulated degree days (DD_5) $5^{o}C$ threshold in Figure 7. Bloom for both varieties has been divided into two periods; before and after peak bloom, and separate equations were used to describe them.

Equations derived from 1981 data of 'Delicious' and 'McIntosh' blossom counts were used to predict the progression of bloom at the MSU Horticulture Farm in 1982. The actual pre-peak bloom curve for 'Delicious' is compared to that predicted from 1981 data in Figure 8a. In 1982 'Delicious' peak bloom

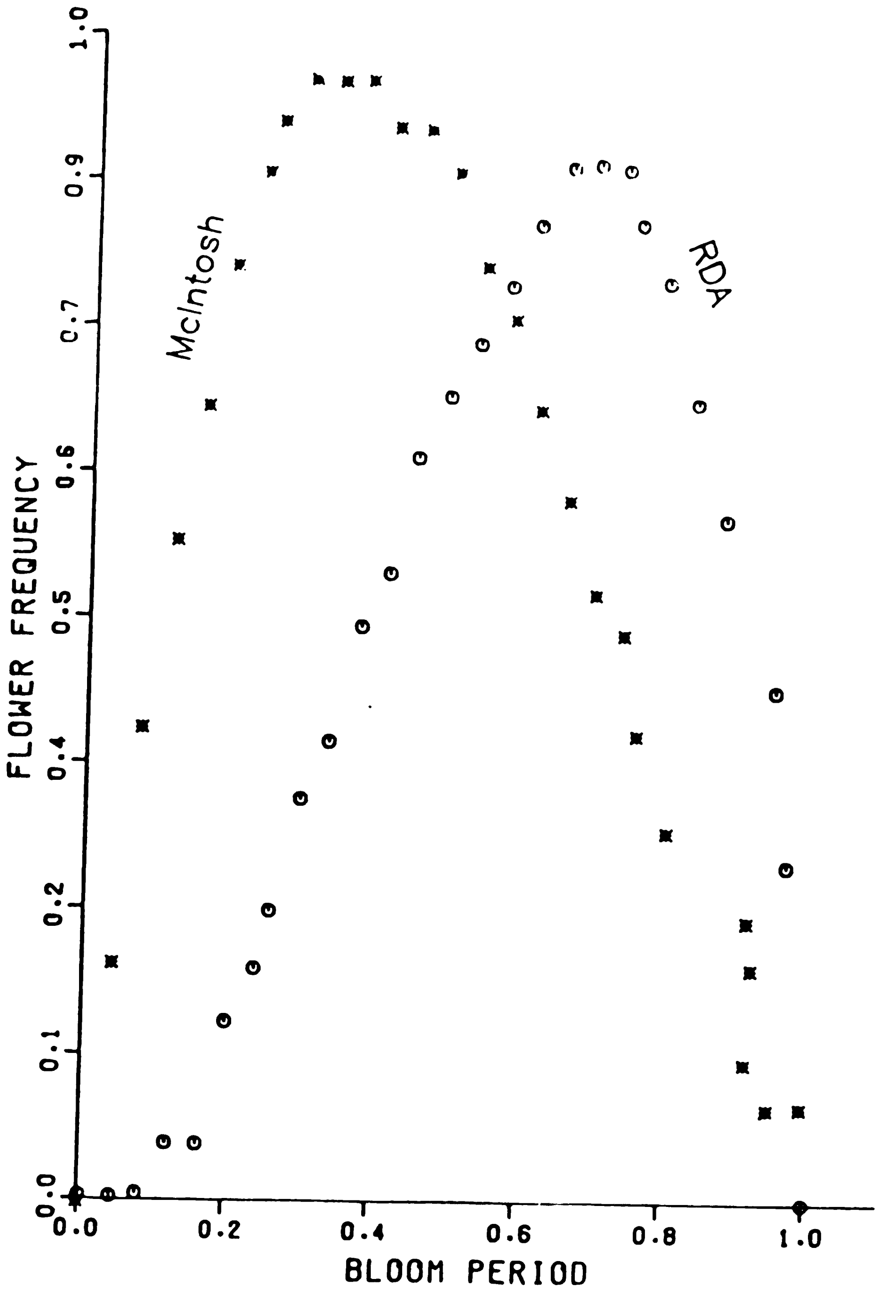


Figure 7. Proposed 'Delicious' and 'McIntosh' bloom curves derived from 1981 field data. (RDA = 'Delicious')

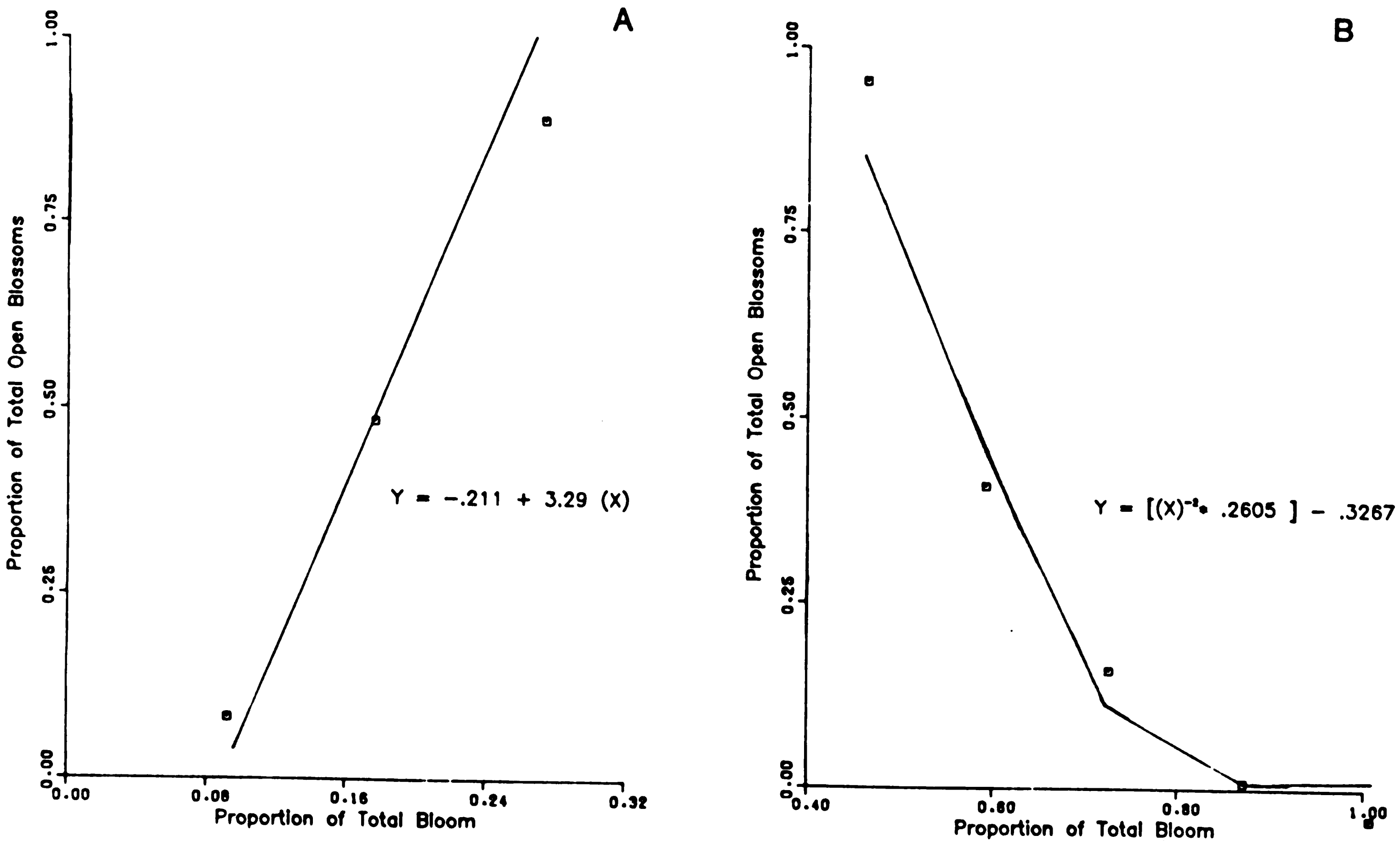


Figure 8. Comparisons of Actual and Predicted Bloom Curves for 'Delicious' (A=Pre-Peak Bloom, B=Post-Peak Bloom) (-=Predicted ▫=Actual).

occurred at 45 DD_5 which was only 2.6 DD_5 later than the average (42.4 DD_5) used for the predictive curve. The model has been programmed to use the integral of the predictive equation: (percentage of open blossoms = -.211 + 3.29 (Accumulated degree days/115) to calculate the number of new blossoms opening each hour. This equation is used by the model from the start of bloom until 60 DD_5 have accumulated.

After peak bloom a second equation is used to predict the progression of bloom: Percentage of total blossoms = $[(DD_5/115)^{-2}*.2605]$ -.3267. This equation was derived from 1981 flower counts at both orchard sites. The comparison of the actual progression of post-peak bloom in 1982 (at the MSU Horticulture Farm) and that predicted by the model is shown in Figure 8b.

In 1981, (at both orchard sites) blossom counts were also made on 'McIntosh' trees, because this variety is often used as a pollinizer for 'Delicious'. Although the general shapes of the 'McIntosh' bloom curves were similar in 1981 and 1982, the percentage of open blossoms at various degree day intervals was quite different using a 5°C base. In 1981 peak bloom occurred at 33.2 DD_5 and 37.9 DD_5 at the MSU Horticulture Farm and Stanek and Son's Orchards respectively. In 1982 peak bloom at the Horticulture Farm did not occur until 43.0 DD_5. Because of the variance in accumulated degree days for peak bloom between the two years, and because the curves for 'McIntosh' derived from 1981 data resulted in such poor estimates for the progression of bloom at a base temperature of 5°C, other base temperatures were tried in an attempt to derive more predictive curves.

At a base temperature of 1.0°C peak bloom in 1981 was found to occur at 52.3DD, at the MSU Horticulture Farm and 49.1DD, at Stanek and Son's orchard.

At the MSU Horticulture Farm in 1982 peak bloom for 'McIntosh' occurred at 54.1 DD_1. Because of the relative similarity of accumulated degree days for peak bloom at the 1.0°C base, and the closer correspondence between the two years in the progression of bloom it is assumed that 'McIntosh' has a lower threshold temperature than 'Delicious', at least for the expression of bloom.

From the 1981 pre-peak bloom data, an equation was derived (using a 1°C base) to predict the progression of bloom in 1982 at the MSU Horticulture Farm. Comparisons of the actual pre-peak bloom curves for 1981 and 1982 with that predicted by the equation are shown in Figure 9a. Peak bloom was predicted to occur at 50.8 DD_1, which is the average of the accumulated degree days for peak bloom for both 1981 and 1982 data.

After 50.9 DD_1 have accumulated, the progression of bloom is predicted by the equation: Percent Bloom = $((DD)^{-2} * .1526) - .148$. Comparisons between bloom curves from this predictive equation and those derived from field data are shown in Figure 9b. With the exception of one point (at 54.5% of the bloom period), the predictive curve lies between or directly in line with the 1981 and 1982 data. As in the case of the 'Delicious' bloom equation, the model uses the integral of these equations to calculate the number of newly opened blossoms during each degree day interval.

Nectar Secretion and Replacement

The average volume of nectar in 'McIntosh' flowers was found to be significantly greater than in 'Delicious' blossoms at both orchard sites in 1981 (Table-1). At Stanek and Sons' orchards 'Delicious' blossoms averaged about 0.024 ml of nectar, while the mean 'McIntosh' nectar secretion was 0.225 ml of nectar per blossom. At the MSU Horticulture Farm 'Delicious' blossoms

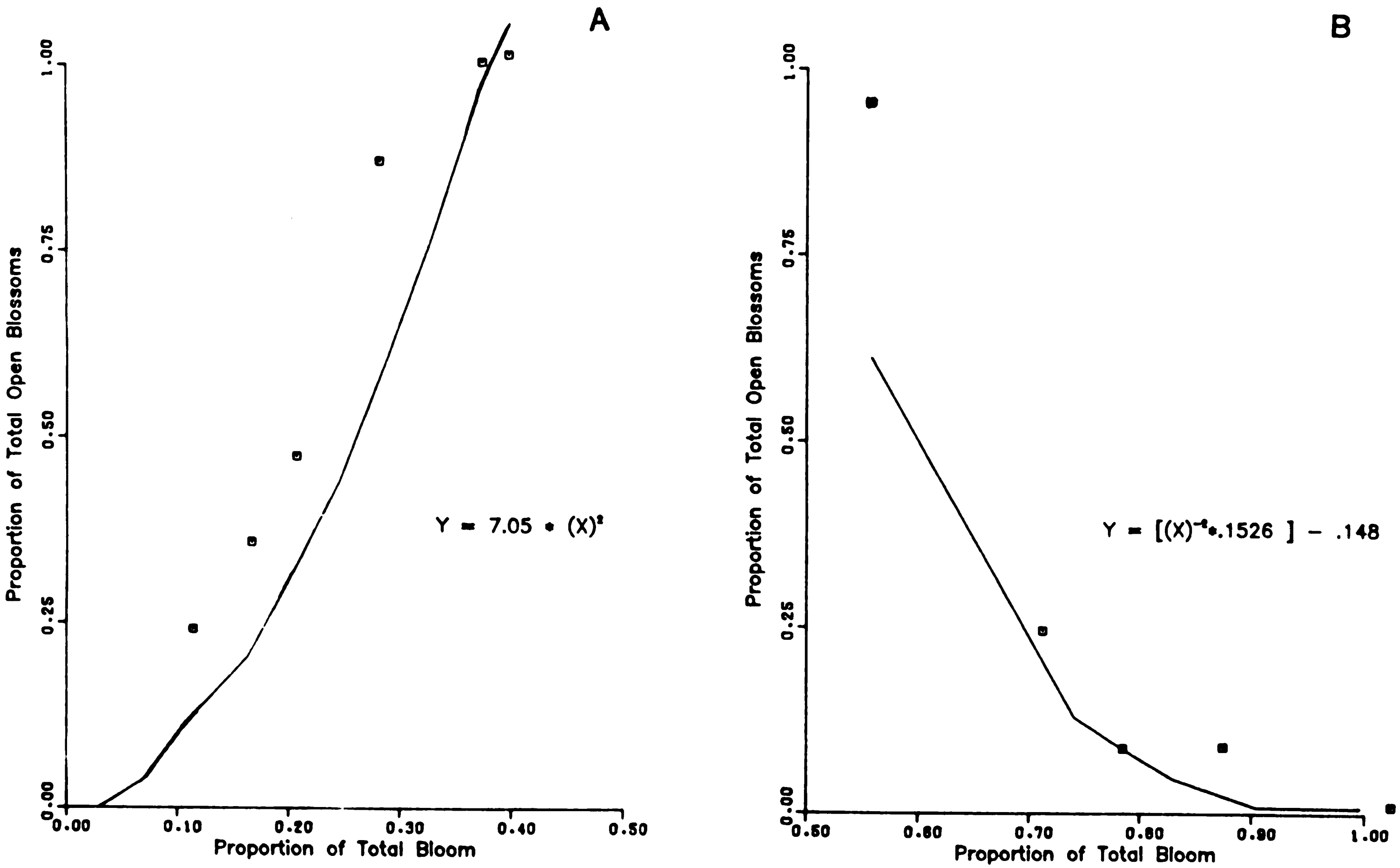


Figure 9. Comparisons of Actual and Predicted Bloom Curves for 'McIntosh'. (A=Pre-Peak Bloom, B=Post-Peak Bloom (-=Predicted, ■=Actual).

Table 1.

Average volume of nectar in apple blossoms on their day of anthesis.

Variety	Site	Sample Size	Average volume of nectar	
'Red Delicious' (Millerspur)	MSU Horticulture Farm	20	.121 ± .08	a
'McIntosh' (MACspur)	MSU Horticulture Farm	20	.337 ± .07	b
'Red Delicious' (Red Chief)	Stanek & Sons'	44	.026 ± .049	a
'McIntosh' (MACspur)	Stanek & Sons'	48	.225 ± .042	b

Means followed by the same letter are not significantly different at the 5% level as determined by Fisher's LSD. Comparisons in nectar volume between sites was not made.

averaged .121 ml of nectar while 'McIntosh' averaged 0.337 ml of nectar per blossom.

The rate of nectar replacement in both varieties was not related to temperature, wind speed, or relative humidity. Although nectar was not secreted at air temperatures below 10°C, the rate nectar was replaced was not found to be a function of increasing temperatures. Even when relative humidity and wind speed, in combination with temperature were used to define the relationship, correlation coefficients for the rate of nectar replacement as it relates to temperature and relative humidity still were less than 0.05 in both varieties.

Originally it was assumed that blossoms would be revisited when their nectar was replaced, and this was predicted to be a function of weather conditions and blossom age. Because this assumption was not supported in the field, blossoms now are predicted to be attractive again 30 minutes after being visited. This assumption is based upon the dissipation time of the "marker" phenomone deposited on blossoms by visiting honey bees (Ribbands 1955). Blossoms are rarely visited by other foragers immediately after a visit, because this pheromone is apparently interpreted as existing exclusively on non-rewarding blossoms. When the pheromone dissipates the blossom can be foraged again and in the case of apples may have replaced all, or none of its original quantity of nectar (according to our data).

The Effects of Bloom on Honey Bees Foraging on Apple

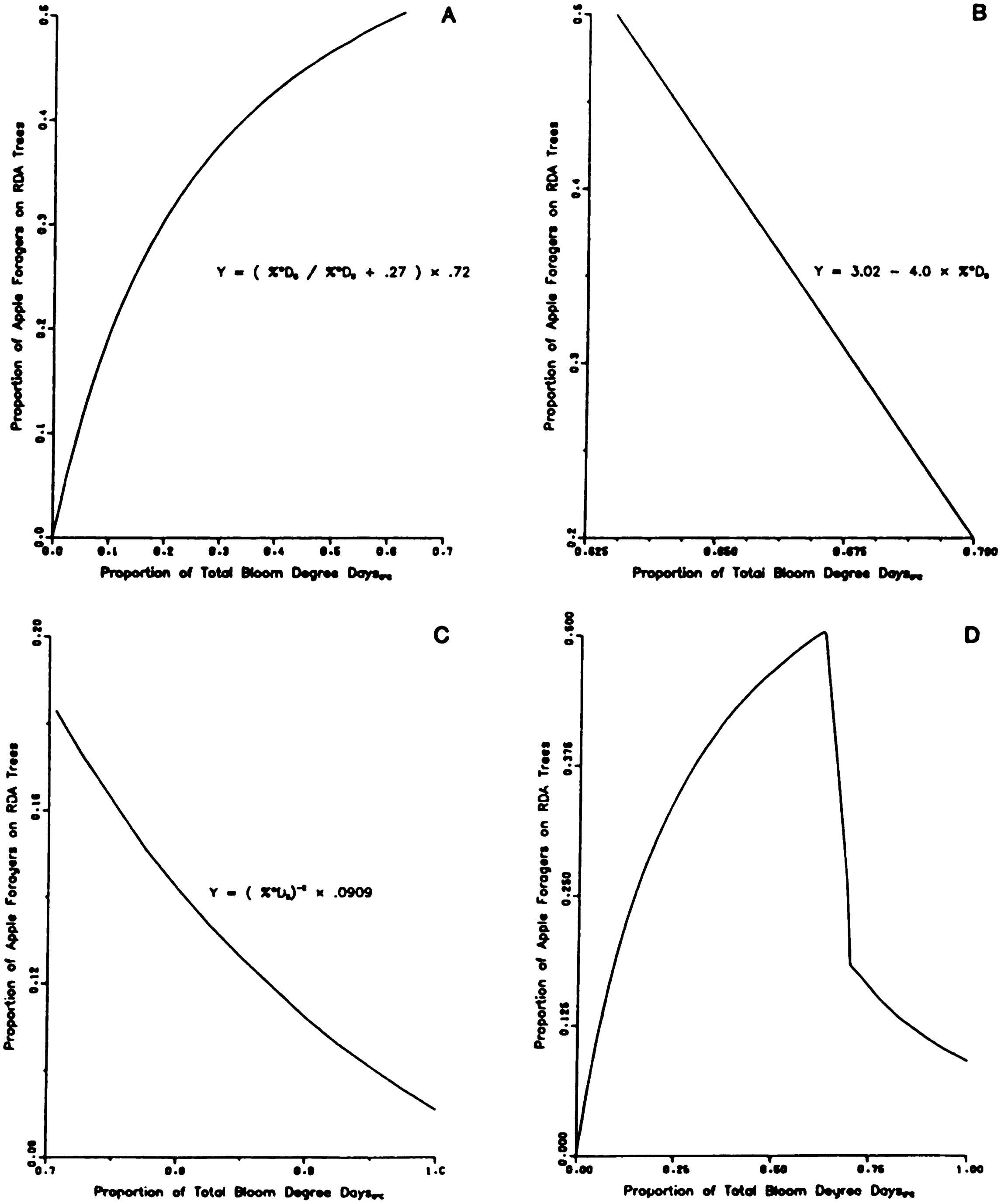
The foraging population response to state of bloom was defined using pollen samples from Erickson-Waller traps (collected in 1981 at the MSU Horticulture Farm), and hourly counts of honey bees on 'Delicious' and 'McIntosh' trees (taken at Stanek and Sons' Orchards in 1982). The curves expressing the relationship between state of bloom (expressed in degree days) and foraging activity are shown in Figures 10d and 11d. Each of these curves is actually a combination of three separate functions whose use is dependent upon the degree day interval (Figures 10 a-c, 11 a-c).

From the start of bloom until just past the bloom peak (i.e. 63% of the 'Delicious' and 40% of the 'McIntosh' bloom expressed) a Michaelis-Menton function best described the foraging response (Figures 10a, 11a). These curves simulate the rapid increase in apple foraging activity after colony introduction as evidenced by Erickson-Waller pollen trap samples. The percentage of apple pollen collected after the first full day of flight averaged 46.4% for four colonies (the percentages of apple and non-apple pollen in the trap was assumed to reflect the percentage of the foraging force on apple). Apple pollen continued to make up about 50% of the pollen in the trap samples as the 'Delicious' and 'McIntosh' trees approached their bloom peaks.

Data from pollen samples were no longer used to predict foraging activity after peak bloom, because later blooming apple varieties ('Golden Delicious' and 'Northern Spy') at the MSU Horticulture Farm were opening at this time, and were being actively foraged. Pollen from trap samples was not identified to variety, therefore these samples could not reflect the decline in foraging activity with the waning of 'Delicious' and 'McIntosh' blooms.

After peak bloom the percentage of the foraging force working 'Delicious' and 'McIntosh' trees was estimated from hourly counts of honey bees on trees at Stanek and Sons' Orchards in 1982. After estimating honeybees/hectare based upon weather and colonies /hectare, the proportion of the foraging force on

Figure 10. Predicted Relationship Between State of Bloom and Foraging Activity on 'Delicious' (A=Pre-Peak Bloom response, B=Post-Peak Bloom Transition response, C=Post-Peak Bloom Response, D=Combined Response Curves).


A
Y = (%*D_s / %*D_s + .27) × .72
Proportion of Apple Foragers on RDA Trees
0.0
0.1
0.2
0.3
0.4
0.5
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
Proportion of Total Bloom Degree Days
B
Y = 3.02 − 4.0 × %*D_s
Proportion of Apple Foragers on RDA Trees
0.2
0.3
0.4
0.5
0.625
0.650
0.675
0.700
Proportion of Total Bloom Degree Days
C
Y = (%*D_s)^-6 × .0909
Proportion of Apple Foragers on RDA Trees
0.08
0.12
0.16
0.20
0.7
0.8
0.9
1.0
Proportion of Total Bloom Degree Days
D
Proportion of Apple Foragers on RDA Trees
0.000
0.125
0.250
0.375
0.500
0.00
0.25
0.50
0.75
1.00
Proportion of Total Bloom Degree Days

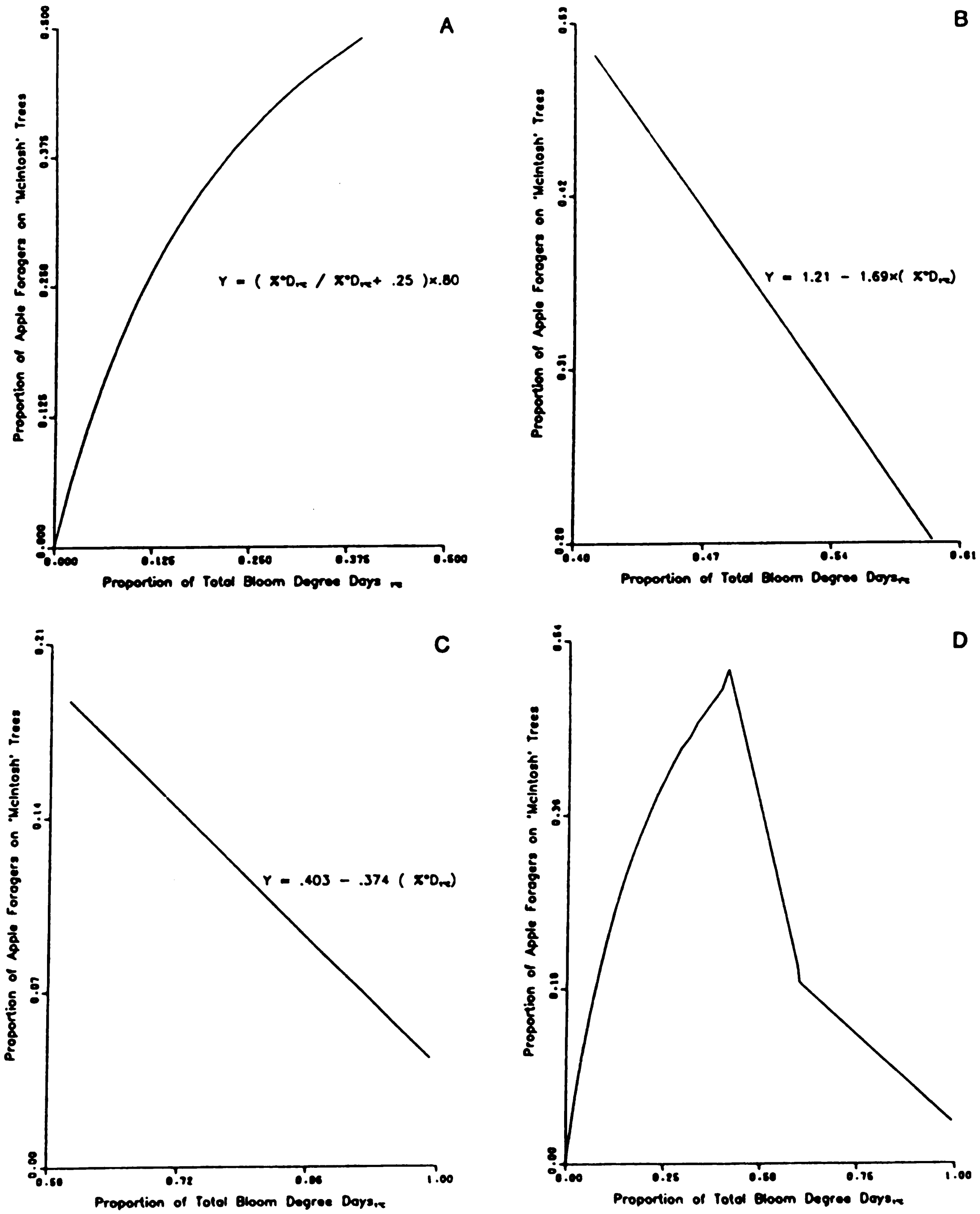


Figure 11. Predicted Relationship Between State of Bloom and Foraging on 'McIntosh' Trees (A=Pre-Peak Bloom Response, B=Post-Peak Bloom Transition Response, C=Post-Peak Bloom Response, D=Combined Response curves).

apple was solved for by testing various percentages until the best predictive curves were acquired. This was accomplished by dividing the post-peak bloom response into two stages; a transition response (for the interval just after peak bloom) and a late bloom response from the end of the transition interval until final petal fall) (Figures 10 b,c and 11 b,c).

Observations of honey bees on 'Delicious' and 'McIntosh' trees after peak bloom showed a decline in the foraging population that was best described using linear functions (Figure 10b and 11b). During this transition interval (defined as the time when 64-70% of the 'Delicious' and 41-59% of the 'McIntosh' bloom was expressed) the bloom was still apparently attractive to a high percentage of field bees, but fractions of the foraging population were abandoning their foraging areas on apple each day.

In the late stages of bloom (the remaining 30% of the 'Delicious' and 41% of the 'McIntosh' bloom), forging activity decreased rapidly on both varieties. The decline in the foraging population on 'McIntosh' was possibly augmented by the proximity of 'Delicious' trees whose bloom was 1-2 days behind 'McIntosh' in its decline. Honey bee working 'McIntosh' trees probably switched to the 'Delicious' rows as the 'McIntosh' bloom declined, and hence brought about an earlier decrease in the foraging population on this variety. The late bloom foraging response for 'Delicious' and 'McIntosh' which gave the best predictions of honey bees on the trees is shown in Figures 10c and 11c.

Predicting Honey Bees per Tree

In 1982 at Stanek and Sons' honey bees were counted (hourly) on 'Delicious' and 'McIntosh' trees, while temperature, solar radiation, and wind speed were recorded. Because of tree size, it was possible to count the bees on the entire tree. An analysis was then conducted to express the influence of weather parameters and state of bloom (expressed in degree days) on honey bee foraging activity on 'Delicious' and 'McIntosh' trees.

Initially a multiple regression was performed on the field data to test if a regression equation could predict foraging activity on apple trees. Although the regression equations for both varieties showed a high degree of correlation between weather, bloom, and bee activity (R^2 values in excess of .85), these equations were not predictive.

The model's original program contained equations derived from the literature describing the influence of temperature, wind, solar radiation, and state of bloom on foraging activity (Jorgensen and Markham 1946, Lundie 1925, cited by Williams and Sims 1977, Free 1960). Honey bees/acre on apple was predicted by removing portions of the maximum possible foraging population using equations derived from these reports. Temperature and solar radiation were reported to have a positive influence on foraging while wind speed had negative affects. State of bloom was reported to positively influence the foraging population before peak bloom and negatively affect it after the bloom peak.

The original program was built on the assumption that a colony during apple bloom averaged 20,000 bees, 8,000 of which were foragers. Predictions of honey bees/tree were made by combining updates on apple foragers/acre (based on weather and state of bloom), and trees of each variety/acre. Comparisons were then made between model output on honey bees/tree using weather data collected at Stanek and Son's Orchard (1982), and actual honey bees/tree at that site under the same weather conditions and degree degree day interval. Unfortunately model predictions were inaccurate and it became apparent that adjustments would have to be made in the equation and assumptions.

After unsuccessful attempts to obtain good prediction using a single equation throughout the day for the honey bee response to solar radiation, it was concluded that the response was dependent upon time of day (i.e. the sun's position on the horizon). This factor apparently influences how positively the foraging population responds to increasing light values. The best foraging population predictions occurred when curves were developed to describe the solar radiation response in the morning, mid-day and afternoon (Figure 12 a,b,c). In the morning (800-1200 hrs daylight savings time (DST)) a linear function with a positive slope, and negative y-intercept (indicating a threshold effect) gave the best honeybees/tree predictions. Between 1300-1400 hrs (DST) the foraging response to solar radiation differed markedly from that in the morning or later afternoon, even when temperature and wind speed remained fairly constant. To account for this, a transition solar radiation curve was derived (Figure 12b), and is used to predict the foraging response during this interval. Finally, a third solar radiation curve was derived to predict foraging activity on apple from 1300 hrs until the end of the flight day (Figure 12c). Field data indicated that the response to light values in the later afternoon differed from those occurring at mid-day (1300-1400 hrs.), and prompted the derivation of this curve.

The foraging response to temperature also required adjustments, and the response function now used in the model is shown in Figure 13a. The program uses a threshold temperature of $10^{\circ}C$ to initiate honey bee foraging on apple. This value was chosen because honey bees were seen foraging apple trees at this temperature, and $10^{\circ}C$ is the threshold for nectar secretion in apple as indicated by our nectar studies. After a temperature of $26^{\circ}C$, it is predicted that honey bee flight no longer is limited by temperature at this time of year.

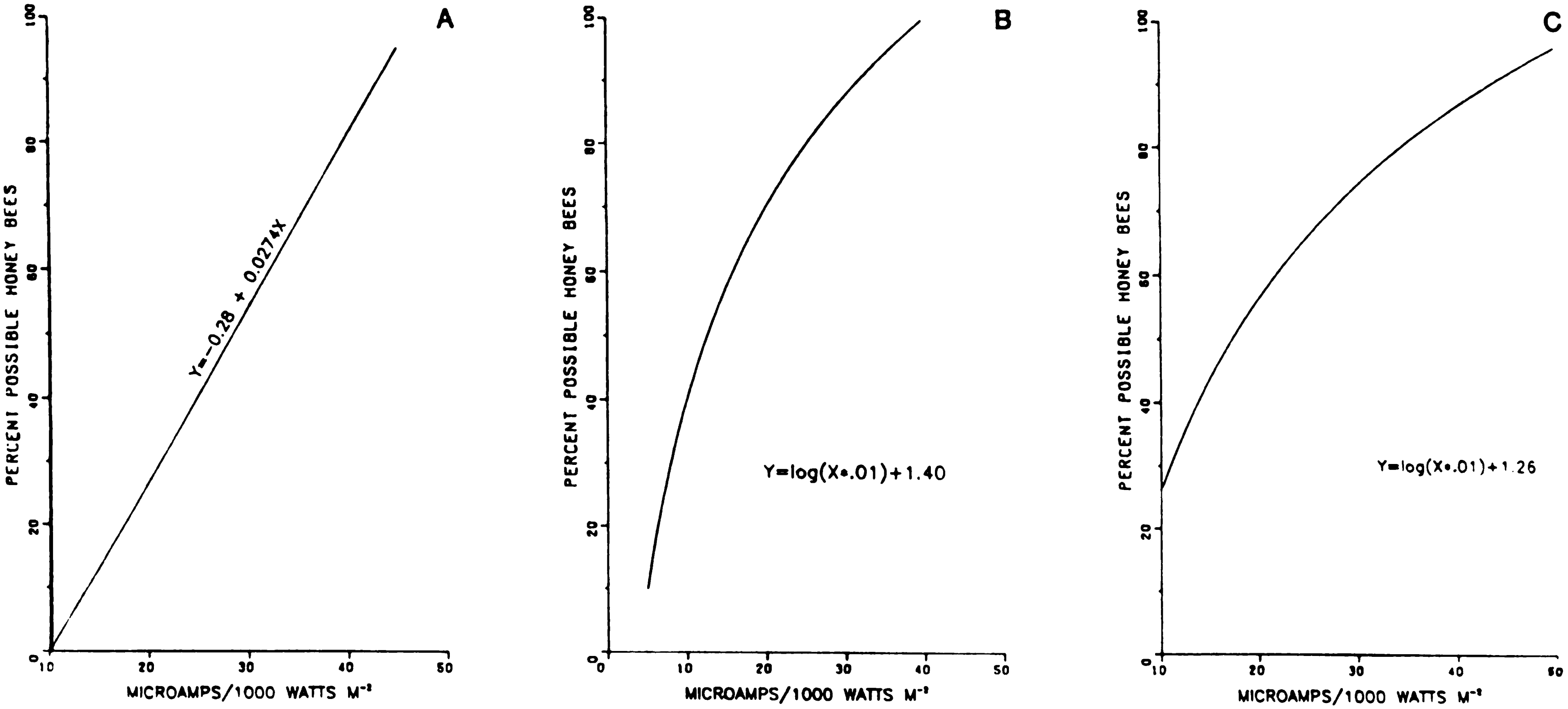


Figure 12. Predicted Honey Bee Flight Response to Solar Radiation Based Upon Time of Day. (A=800-1200 Hours, B=1300-1400 Hours, C=1500-Sunset).

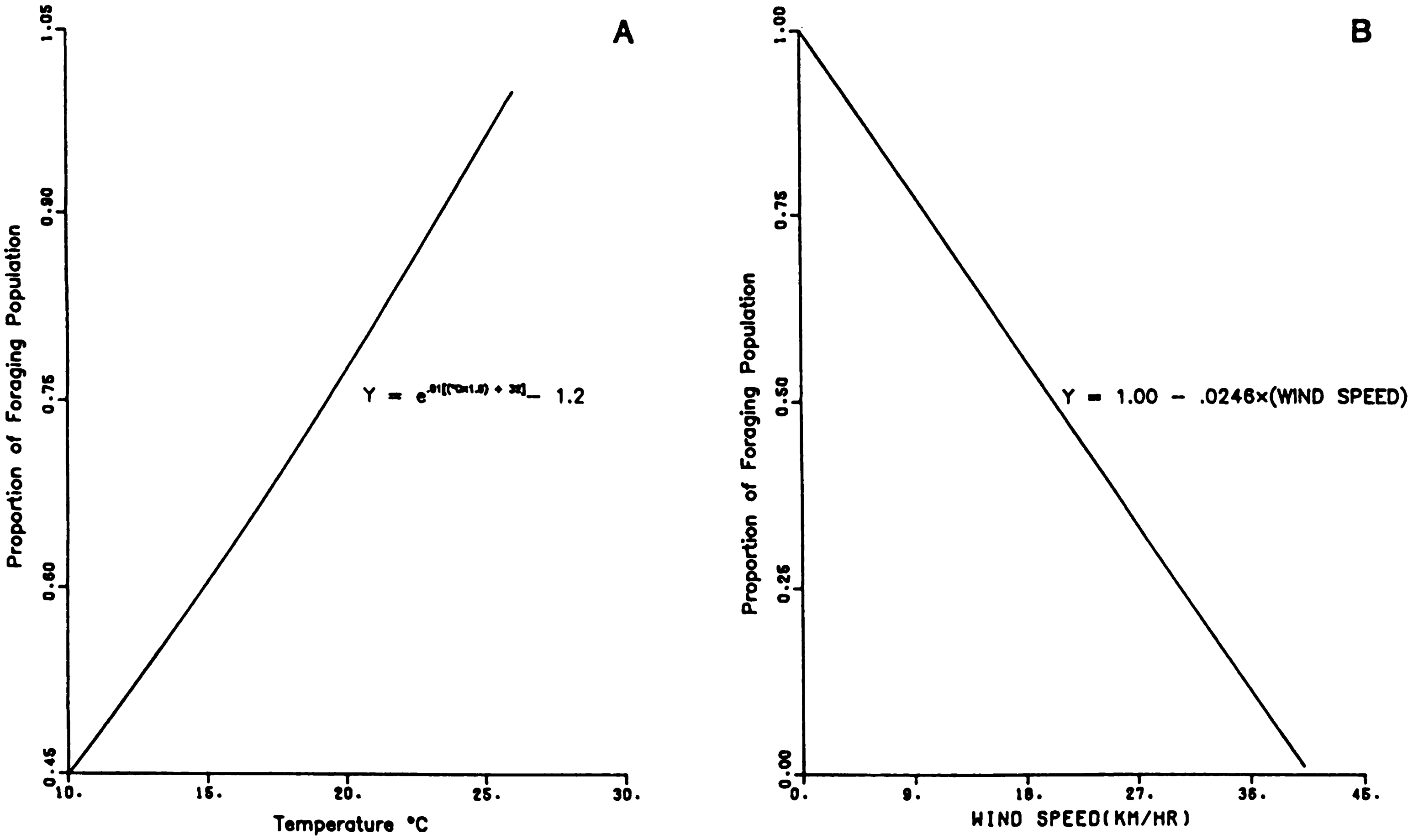


Figure 13. The Predicted Foraging Response to Temperature (A) and Wind Speed (B).

The curve expressing the relationship between wind speed and foraging on apple is a hybrid of our data and literature values (Figure 13b). Originally a negative exponential curve was fitted to the literature data, but was found to severely underestimate flight activity. The linear function shown in Figure 14b gave far more accurate predictions of honey bees/tree when used in concert with the temperature and solar radiation curves. The lower and upper limits of the curve are from literature reports, while values in between are a product of field data and simulation runs (Brittain 1933 cited by Free 1960, Rashad 1957).

It was initially assumed that a colony contained about 8,000 foragers, but the accuracy of this assumption needed testing. At Stanek and Sons' Orchard 56 colonies (54 rented colonies and two from the University apiary) were introduced at a density of .11 colonies/hectare. Colonies were composed of two standard depth hive bodies, and were a combination of overwintered colonies and early spring starts from packaged bees. Taking into account colony density/hectare, a series of calculations were performed to approximate the number of foragers/colony. The combination of hourly counts of honey bees/tree and number of trees per hectare was used to estimate the number of honey bees working apple/hectare. Using the percentages of apple and competitive plant pollen coming into the hive from pre-peak bloom pollen sample data (from the Erickson-Waller traps), the approximate portion of the total honey bees/acre foraging apple was calculated for a particular degree day interval. Possible apple foragers per acre was then calculated by correcting for the decrease in the foraging population due to weather (during the sampling period). The total number of foragers per colony was then estimated by adding the portion of the total foraging population on apple to the remaining percent on competitive plants and dividing by .11 colonies/hectare. Estimates of foragers/colony were made by repeating this procedure at various sampling intervals. From our data is was estimated that colonies had between 4500-4600 bees in their foraging population.

Comparisons of actual honey bees on 'Delicious' and 'McIntosh' trees (under monitored weather conditions) and those predicted by the model are shown in Figures 14a,b. On both 'Delicious' and 'McIntosh' trees, predictions of bee activity during the morning and late afternoon are by far the most accurate: (actual 'Delicious' honeybees-predicted)^2 = 0.511, (actual 'McIntosh' honey bees - predicted).^{2} = .208). Only from 1300-1400 hrs do the predictions become less precise: (actual 'Delicious' honey bees -predicted)^2 = 0.626, (actual 'McIntosh' honey bees - predicted)^2 = 0.420).

Analysis of Pollens on Apple Foragers and Blossom Stigmata

Pollen from various apple varieties and competitive plants blooming concurently with 'Delicious' and 'McIntosh' trees could be identified by size and exine pattern using SEM (Figures 15 and 16). Pollen samples collected from the bodies of apple foragers were compared to those collected from 'Delicious' and 'McIntosh' trees. Pollen types were then identified as being self-, cross-, or non-apple pollen relative to the tree (or plant) from which the bee was collected. In 1982 every honey bee captured while working 'Delicious' or 'McIntosh' trees (at the MSU Horticulture Farm) was carrying pollen from other apple varieties and in some instances pollen from other plant species (Figure 17) (Table 2). Three honey bees captured while foraging dandelion flowers were also found carrying pollen types other than dandelion.

'Delicious' foragers captured both in the morning (900-1200 hrs DST) and afternoon (1300-1750 hrs DST) were found to have significantly more compatible

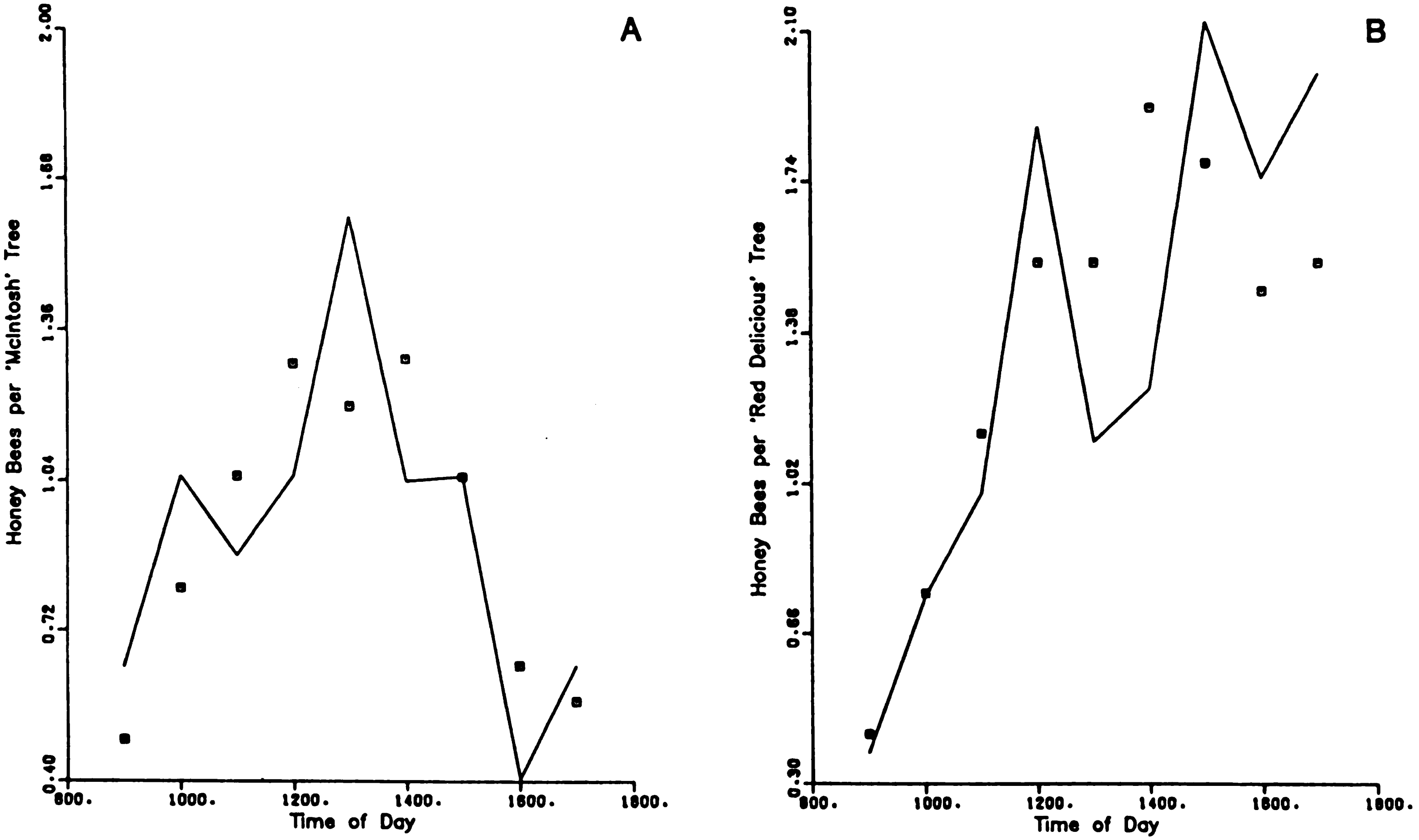


Figure 14. Actual and Predicted Honey Bees Per Tree During a Nine Hour Foraging Period (A=Honey Bees/'McIntosh' tree, B=Honey Bees/'Delicious' Tree) (-=Actual, ▪ =Predicted).

Figure 15. Scanning electron micrographs of apple pollen grains. A = Millerspur 'Delicious' (1800x), B = Macspur 'McIntosh' (1800x), C = 'Gallia' (1800x), D = 'Rhode Island Greening' (1800x).

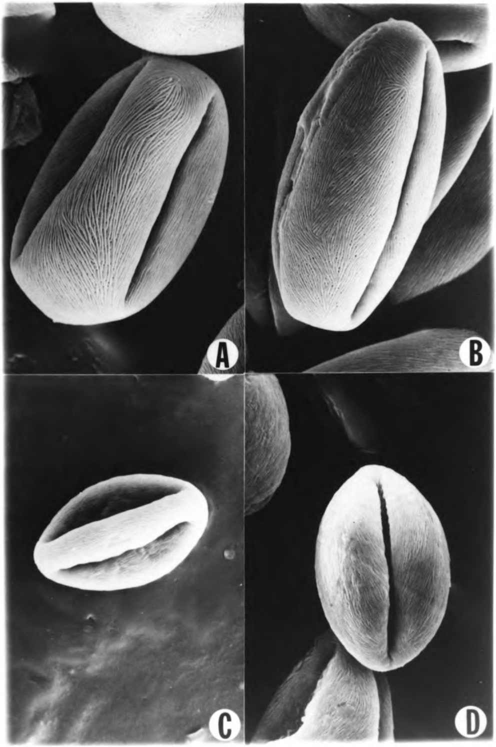

A
B
C
D

Figure 16. Scanning electron micrographs of pollen from species blooming in concert with apple. A = Tart Cherry (720x), B = Stanely Plum (720x), C = Bartlett Pear (1800x), D = Bosc Pear (660x), E = Dandelion (*Taraxacum* spp) (440x), F = Yellow rocket (*Barbarea* spp) (1300x).

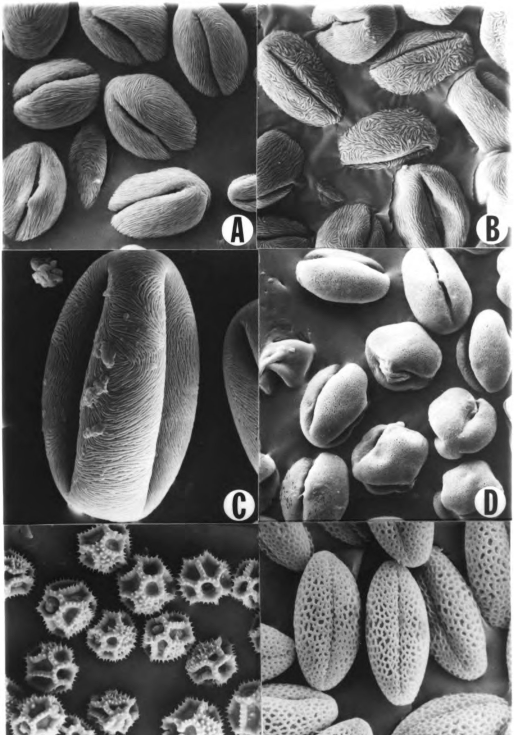

A
B
C
D
E
F

Figure 17. Scanning electron micrographs of pollen carried by honey bees foraging 'McIntosh' trees at the Michigan State University Horticulture Farm.

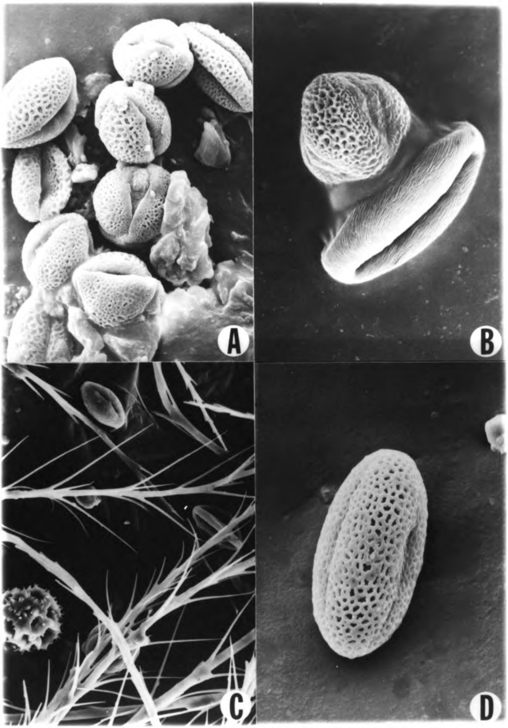

A
B
C
D

Table 2

Percentages of self-, cross-, and non-apple pollen on the bodies of honey bees foraging apple blossoms at the MSU Horticulture Farm.

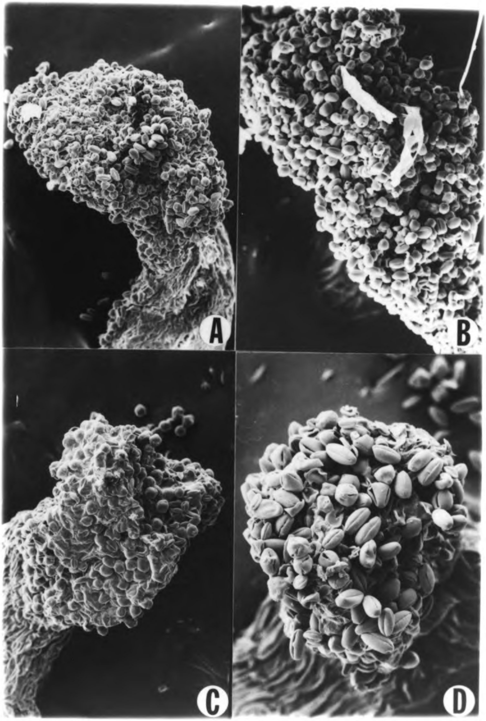
Variety Being Foraged	Sample Size	Time	% self pollen	% cross pollen	% non-apple pollen
'Red Delicious'	7	AM	22.7 ± 18.8 a	55.7 ± 18.3 b	21.6 ± 22.0 a
	10	PM	9.70 ± 7.00 a	55.0 ± 14.0 b	35.3 ± 15.6 b
'McIntosh'	9	AM	31.5 ± 15.4 a	46.6 ± 17.5 a	21.9 ± 14.5 a
	5	PM	4.70 ± 6.80 a	68.3 ± 38.2 b	27.0 ± 41.4 a
Combined 'Red Delicious and 'McIntosh' foragers	16	AM	27.6 ± 10.6 a	50.6 ± 11.3 b	21.8 ± 10.9 a
	15	PM	8.2 ± 5.0 c	58.8 ± 12.1 b	32.9 ± 12.1 a

Means followed by the same letter are not significantly different at the 5% level as determined by Fisher's LSD pollen (i.e. pollen from an unrelated variety) than self-pollen on their bodies (Table 2). Honey bees captured while working a solid block of 'McIntosh' trees (at the MSU Horticulture Farm) were also carrying both self and compatible pollen, but in different proportions in the morning and afternoon (Table 2). Compatible pollen was predominant during afternoon hours only on these 'McIntosh' foragers, and was present in approximately equivalent amounts to self- and non-apple pollen in the morning.

Although significantly more compatible pollen was found on both 'Delicious' and 'McIntosh' foragers, the small sample sizes warrant conservative conclusions, concerning the mean percentages of pollen types. At the very least though, honey bees captured on both varieties were found to be in a condition where cross pollination was possible if at least some of the pollen on the bee's body was viable. Even when trees were planted in a solid block arrangement (as in the case of the 'McIntosh' trees), honey bees were carrying pollen on their bodies from apple varieties that were located several hundred meters away. When all samples were combined, compatible pollen was found to comprise the majority of pollen types carried on a forager's body in both the morning and afternoon (Table 2).

The foragers ability to transfer compatible pollen was evidenced by its presence on the stigma (Figure 18). In these samples the stigmatic surface was often heavily coated with pollen, so that only those grains on the outer most surface could be counted. All pollinated stigmata collected from 'Delicious' and 'McIntosh' trees at both the MSU Horticulture Farm and Stanek and Sons' Orchards were found to contain compatible pollen grains (Table 3). Whether compatible pollen actually existed directly on the stigmatic surface, and hence

Figure 18. Scanning electron micrographs of pollinated apple blossoms stigma: A and B from 'McIntosh' blossoms, while C and D are from 'Delicious'.



stigma:
Delicious

Table 3

Percentages of 'Red Delicious' and 'McIntosh' stigmata containing self-, cross-, and non-apple pollen at the MSU Horticulture Farm.

Variety	Sample Size	% with pollen	% with self-pollen	% with cross-pollen	% with non-apple pollen
'Red Delicious'	15	73.3	91.0	100.0	18.2
'McIntosh'	11	81.8	77.8	100.0	11.1

was in a position to germinate and ultimately fertilize ovules could not be determined with the SEM procedure.

From these field results, a new subroutine called "In Hive" was added to the model to predict the number of pollinators arising from pollen transfer among nestmates in the hive. The flow diagram describing this subroutine is shown in Figure 19. The number of honey bees leaving the hive carrying pollen that could set fruit on 'Delicious' or 'McIntosh' trees is predicted to be a function of uninterrupted foraging intensity (number of honey bees leaving the hive) during the previous hours as described by the equation: % of honey bees with mixed pollen (in the current hour) = .213 * $\log_{10}$ (number of foragers leaving the hive the previous hour) (Figure 20). The number of possible cross pollinators (at time (t)) is then obtained by multiplying the percentage of bees with mixed pollen by the number of foragers leaving the hive that hour.

Although honey bees may acquire pollen in the hive, unless it is from a variety that is compatible with either the pollinizer or 'Delicious', these bees cannot be added to the pollinator population. The potential pollinator population is predicted to be a function of both foraging intensity and the percentage of the foraging population working either 'Delicious' or pollinizer trees. The percentage of the foraging population on these varieties (as predicted by accumulated degree days and state of bloom) is assumed to reflect the percentage of pollen types coming into the hive, and hence the probabilities of an apple forager leaving the hive with compatible pollen. Consequently as the number of foragers on the pollinizer and 'Delicious' trees increases, the amount of these pollens entering the hive increases, raising the probability that apple foragers will obtain compatible pollen within the hive by contact with nestmates.

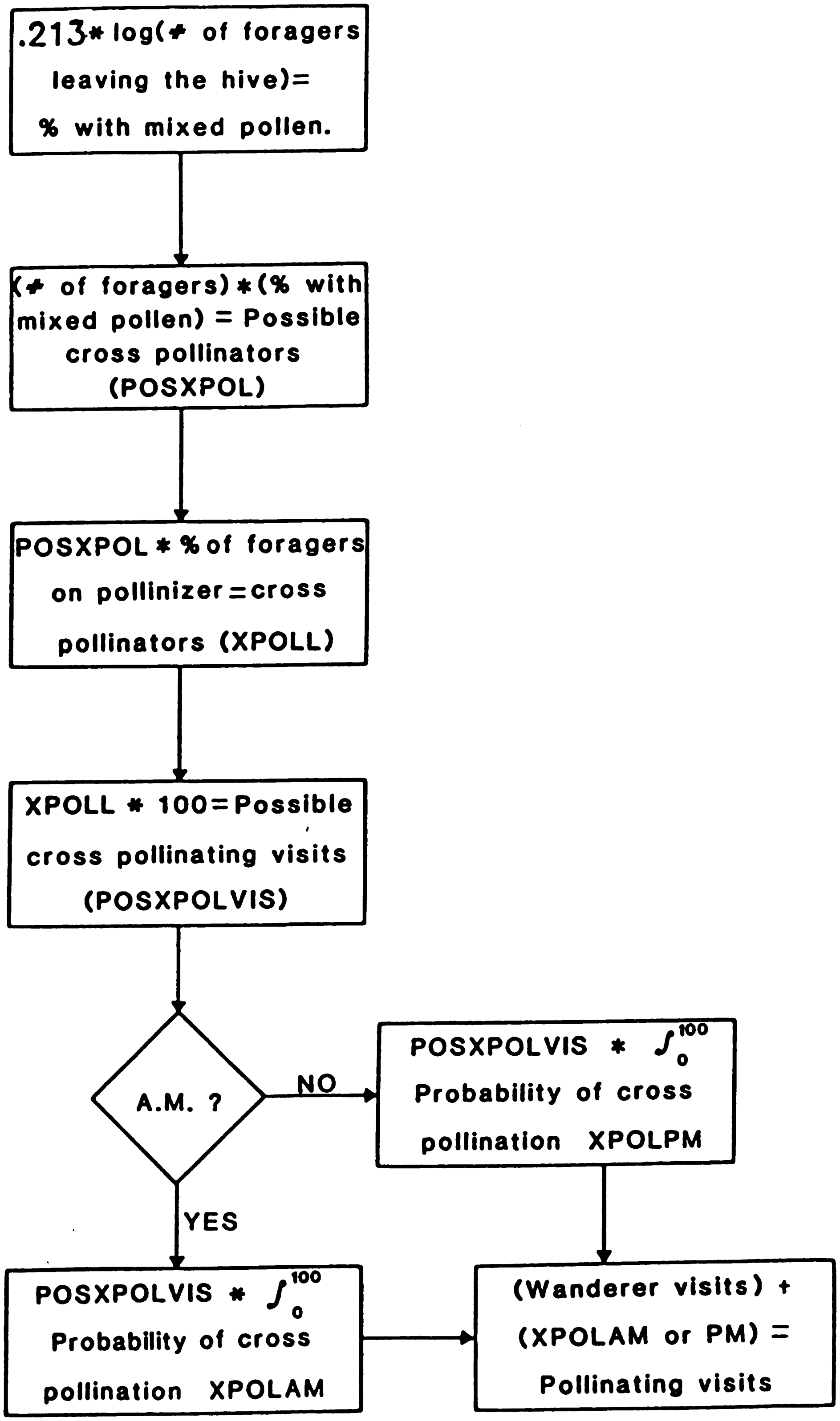


Figure 19. Sequence in the "In Hive" Subroutine.

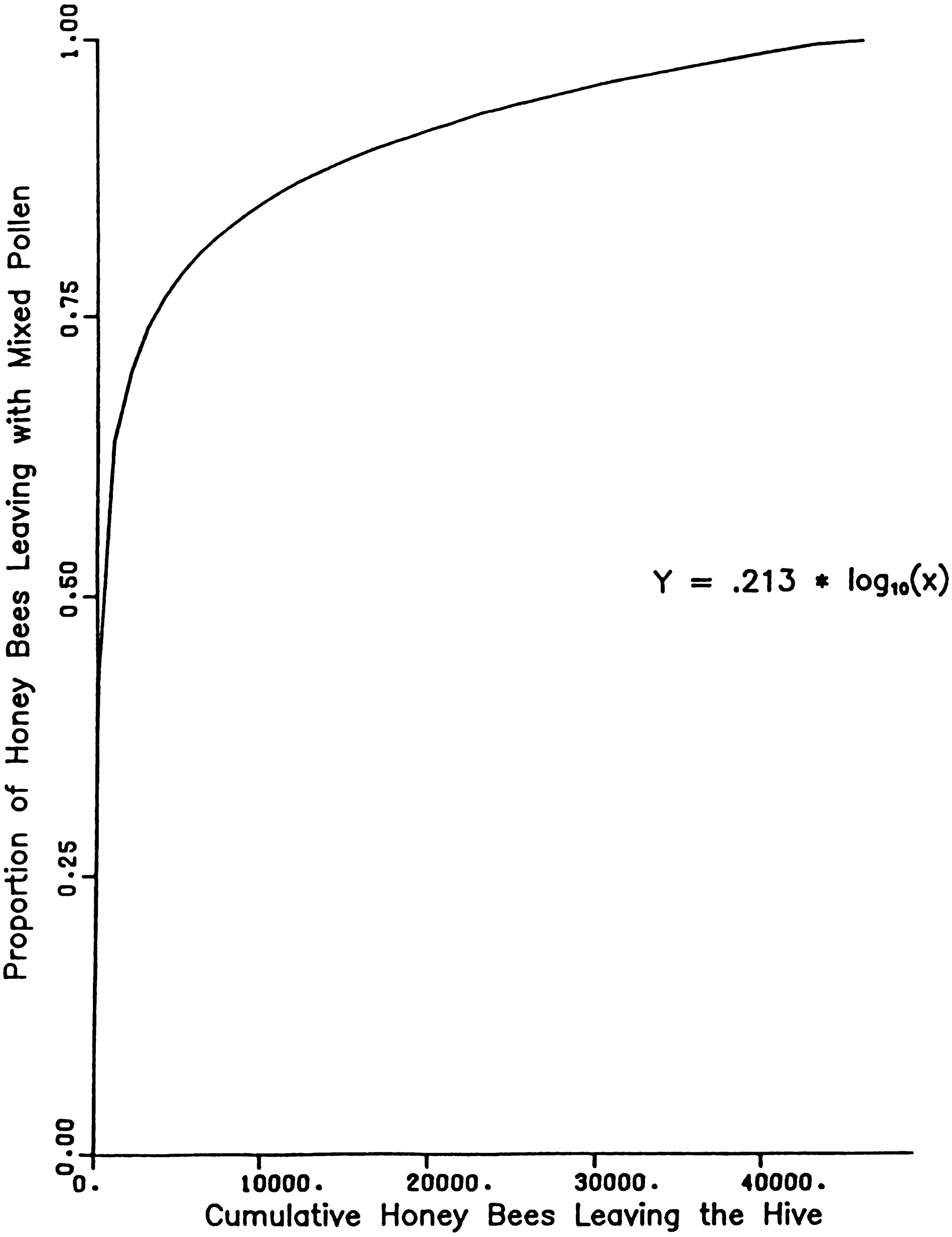


Figure 20. Predicted In-Hive Pollen Transfer Rate as a Function of the Cumulative Honey Bees Leaving the Hive During the Day.

Honey bees were timed while working 'Delicious' and 'McIntosh' trees to determine the average number of blossoms visited per hour. After accounting for travel time and transfer of pollen and nectar loads to bees in the hive, foragers were estimated to be visiting an average of 100 apple blossoms/hour. The possible cross pollinating visits in an hour is then predicted to be the number of cross pollinating bees (i.e. foragers that have acquired compatible pollen in the hive or by moving from tree to tree) estimated that hour multiplied by 100 visits.

Because pollen was shed primarily in the morning in the orchards used in this study, compatible pollen acquired in the hive would be more rapidly diluted by self-pollen during this time if foragers were working a single variety (either 'Delicious' or pollinizer). Consequently, although a honey bee may visit about 100 blossoms per foraging trip, she probably only cross pollinates a variable percentage based upon time of day. Finally the total pollinating visits occurring in an hour is predicted to be the sum of those performed by wandering bees moving from the pollinizer to the 'Delicious' trees (or 'Delicious' trees to the pollinizer), and visits by honey bees that have acquired compatible pollen in the hive.

Effect of Blossom Density on Fruit Set

In 1981 at the MSU Horticulture Farm, 'Delicious' trees with sparse flowering had a July fruit set (Fruit/Blossom) that ranged between 0.35 and 0.83 depending upon blossom density (Figure 21a) 'McIntosh' trees had a higher blossom density than 'Delicious', and had lower initial fruit sets (0.042 - 0.174) (Figure 22a). In both varieties there was an inverse relationship between blossom density and initial fruit set that resembled a negative exponential function.

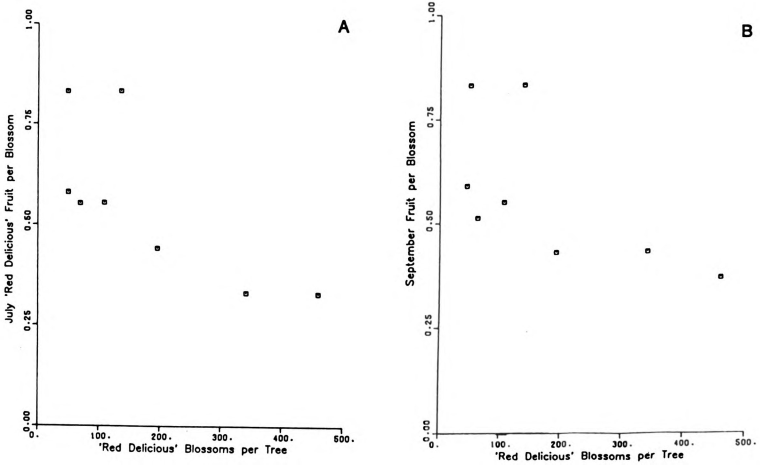


Figure 21. The relationship between blossom density and fruit set in 'Delicious' (MSU Horticulture Farm 1981).

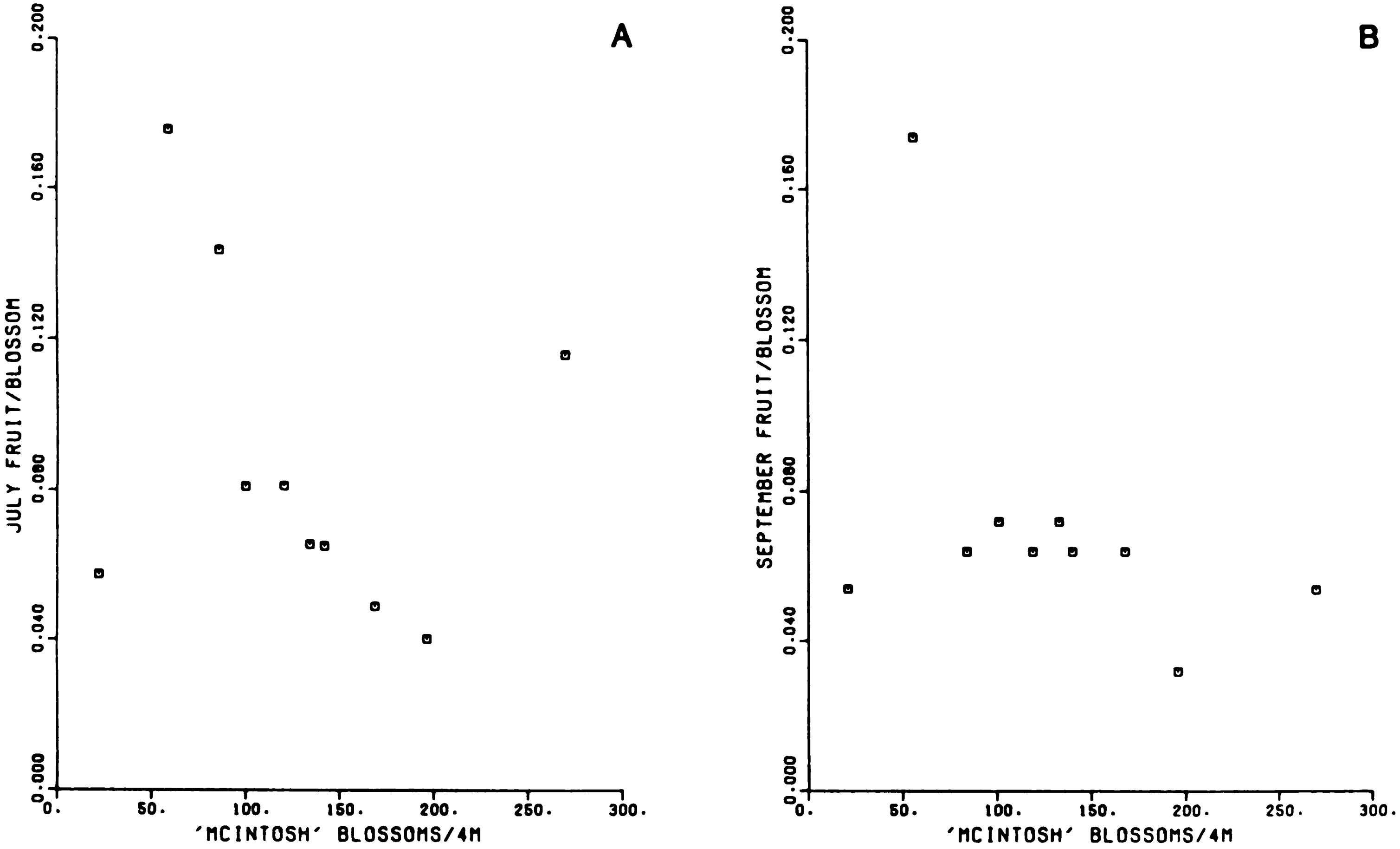


Figure 22. The Relationship Between Blossom Density and Fruit Set in 'McIntosh'. (MSU Horticulture Farm 1982) (A=June Fruit Set, B=September Fruit Set).

Throughout the 1981 season, 'McIntosh' trees continued to self thin, thus reducing their initial fruiting percentages. Thinning occurred in 'Delicious' trees too, but to a much lesser extent, especially in trees with very few flowers. By harvest time the 'Delicious' flowering to fruiting curve had not changed in shape (Figure 21b). In contrast, 'McIntosh' trees considerably reduced their initial fruit set so that the final fruit set curve appeared linear (with the exception of one point) with fruit set percentages ranging between 0.03 and 0.08 (Figure 22b)

In 1982 this experiment was repeated at the MSU Horticulture Farm and Ashby's Orchard using trees of different blossom densities. Again there was a trend where an inverse relationship existed between initial set and flower density in both 'Delicious' and 'McIntosh' trees (Figures 23 and 24). 'Delicious' blossom density (at the MSU Horticulture Farm) ranged between 82 and 143 blossoms/meter, and had a respective initial fruit set range of 0.18-0.34 (Figure 23a). Blossoms per meter of branch on 'McIntosh' trees ranged between 52 and 126, and had an initial fruit set range of 0.06-0.24 (Figure 24a).

Self-thinning occurred in both varieties throughout the season so that final fruit set ranges for 'Delicious' and 'McIntosh' at the MSU Horticulture Farm were 0.11-0.21 and 0.04-0.13 respectively (Figures 23b and 24b). Final fruit set rates in both varieties did not appear to be as strongly influenced by blossom density in 1982 as 1981 particularly in the 'Delicious' trees. This could have occurred because blossom density on 'Delicious' trees in 1981 was much lower than in 1982 (in 1981 blossoms on the entire 'Delicious' tree were counted for this experiment, while in 1982 this was not feasible because of the higher blossom density). At very low blossom density levels flowering could have a more pronounced effect on both initial and final fruit set, while in instances when all

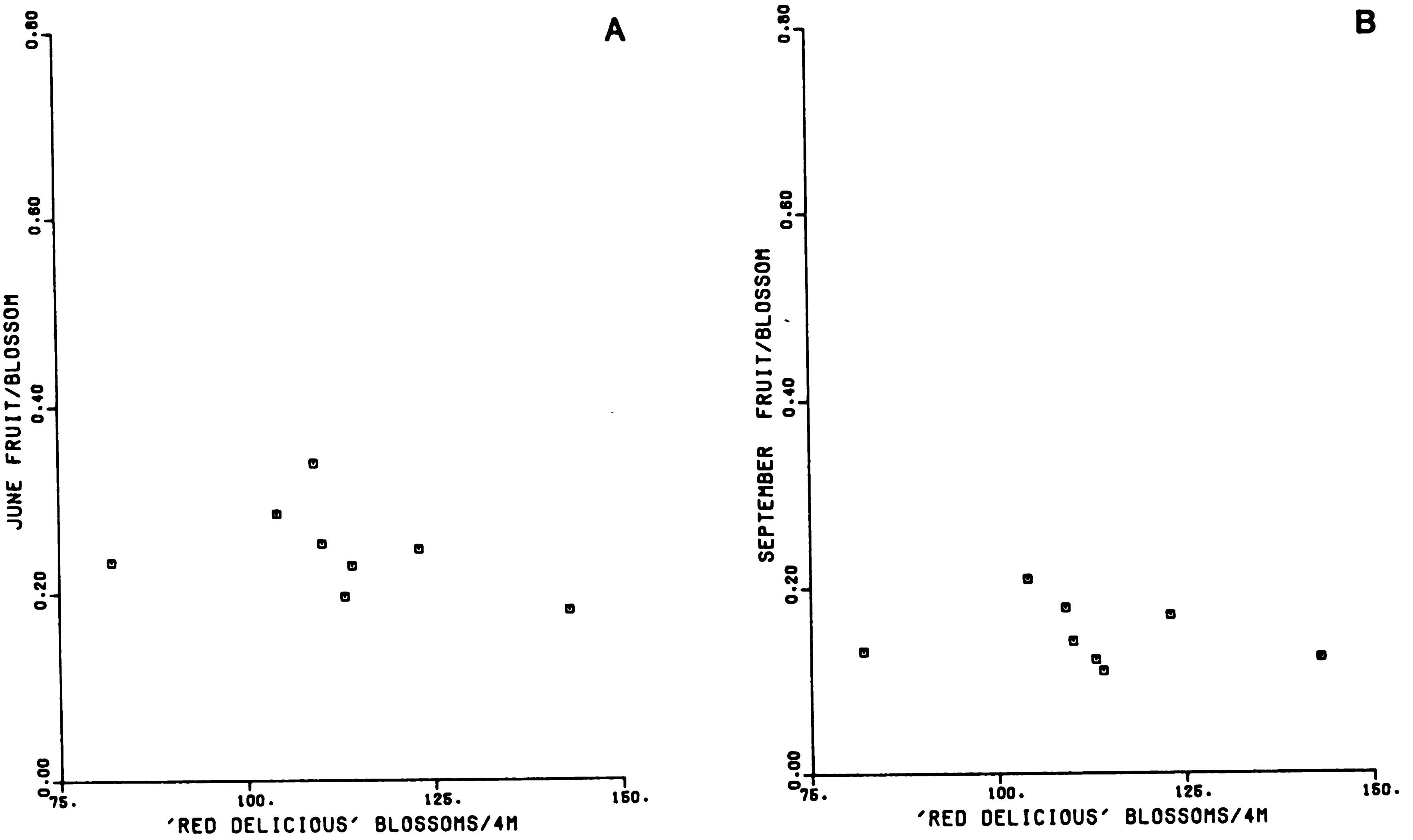


Figure 23. The Relationship Between Blossom Density and Fruit Set in 'Delicious' (M.S.U. Horticulture Farm 1982) (A = June Fruit Set, B = September Fruit Set).

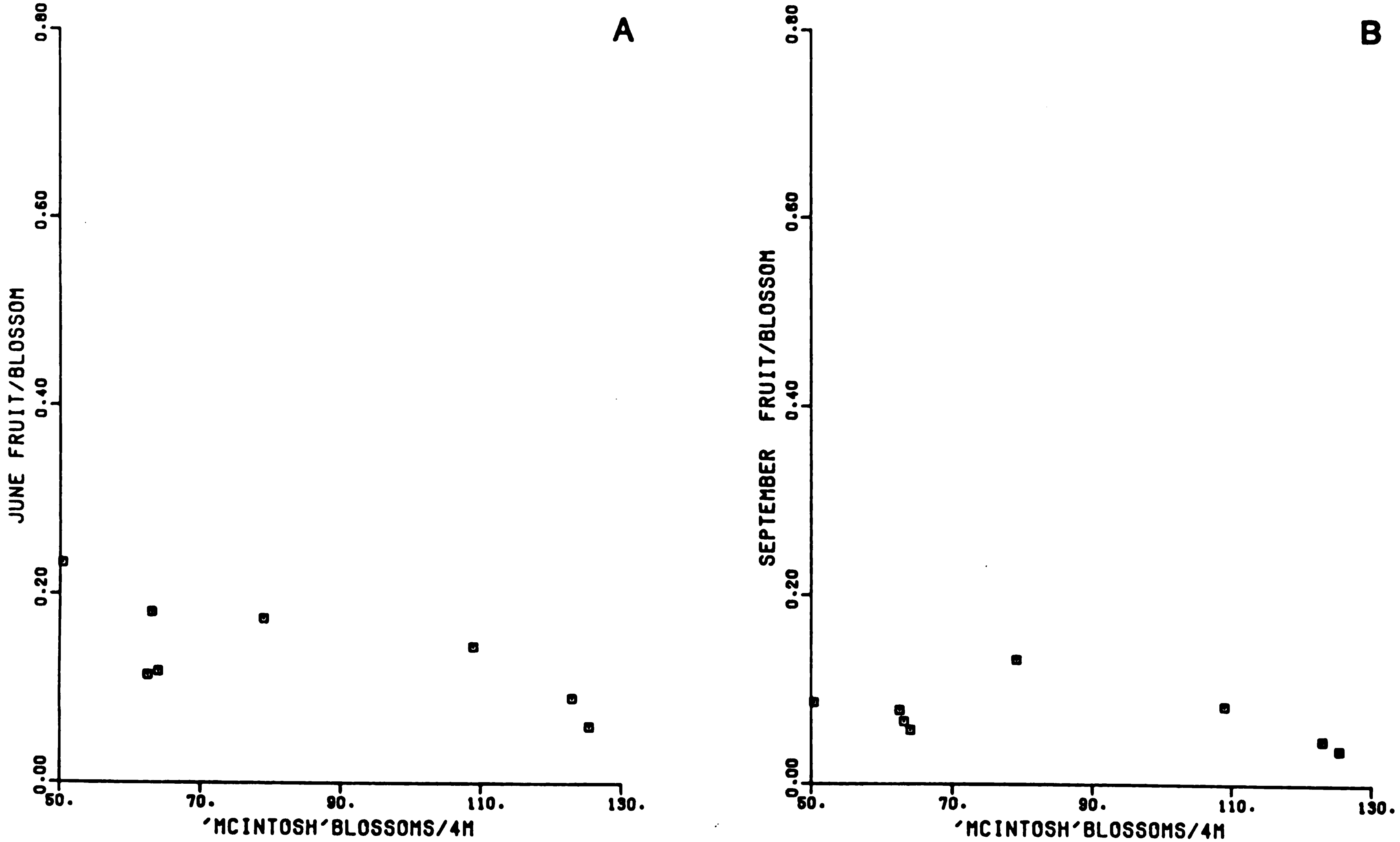


Figure 2.4. The Relationship Between Blossom Density and Fruit Set in 'McIntosh'. (MSU Horticulture Farm 1982) (A=June Fruit Set, B=September Fruit Set).

trees have comparatively high blossom density, the resulting fruit set range is considerably narrower.

Further testimony is added to this conclusion by considering the data collected at Ashby's orchard in 1982. Trees at this site were only 2-3 m tall so blossoms on the entire tree could be counted. Flowering was relatively dense on both 'Delicious' and 'Empire' trees (relative to their size), and ranged between 200-980 blossoms/tree on 'Delicious' and 800-1830 blossoms/ tree on the 'Empire.' Initial and final fruit sets on 'Delicious' ranged between 0.018-0.072 and 0.012-0.066 respectively, but did not show a marked influence of blossom density on the fruit set rate (Figure 25). Even in the 'Empire' trees where there was a comparatively wide range in blossom density between trees, initial (0.048-0.066) and final (0.036-0.066) fruit set rates did not show an influence of blossom density on final fruiting (Figure 26) The trend of trees with lighter flowering showing less thinning did hold true for this site though, as it did for data collected at the MSU Horticulture Farm.

Results from these experiments were incorporated into the model to establish initial fruit set goals for the grower. At both Ashby's Orchards and the MSU Horticulture Farm, thinning sprays were not applied, and final fruit size was suitable in size for fresh market. When growers using the model input blossom density/meter of branch (on their 'Delicious' trees), an ideal fruit set percentage based upon the equation: $\text{fruit/blossom} = e^{-0.002(\text{blossoms/m})} - 0.4503$ (Figure 27) is established as a pollination goal for this variety. If 'McIntosh' is used as a pollinizer the equation used to establish the fruit set goal is: $\text{fruit/blossom} = e^{-0.0018(\text{blossoms/m})} - 0.70$ (Figure 28).

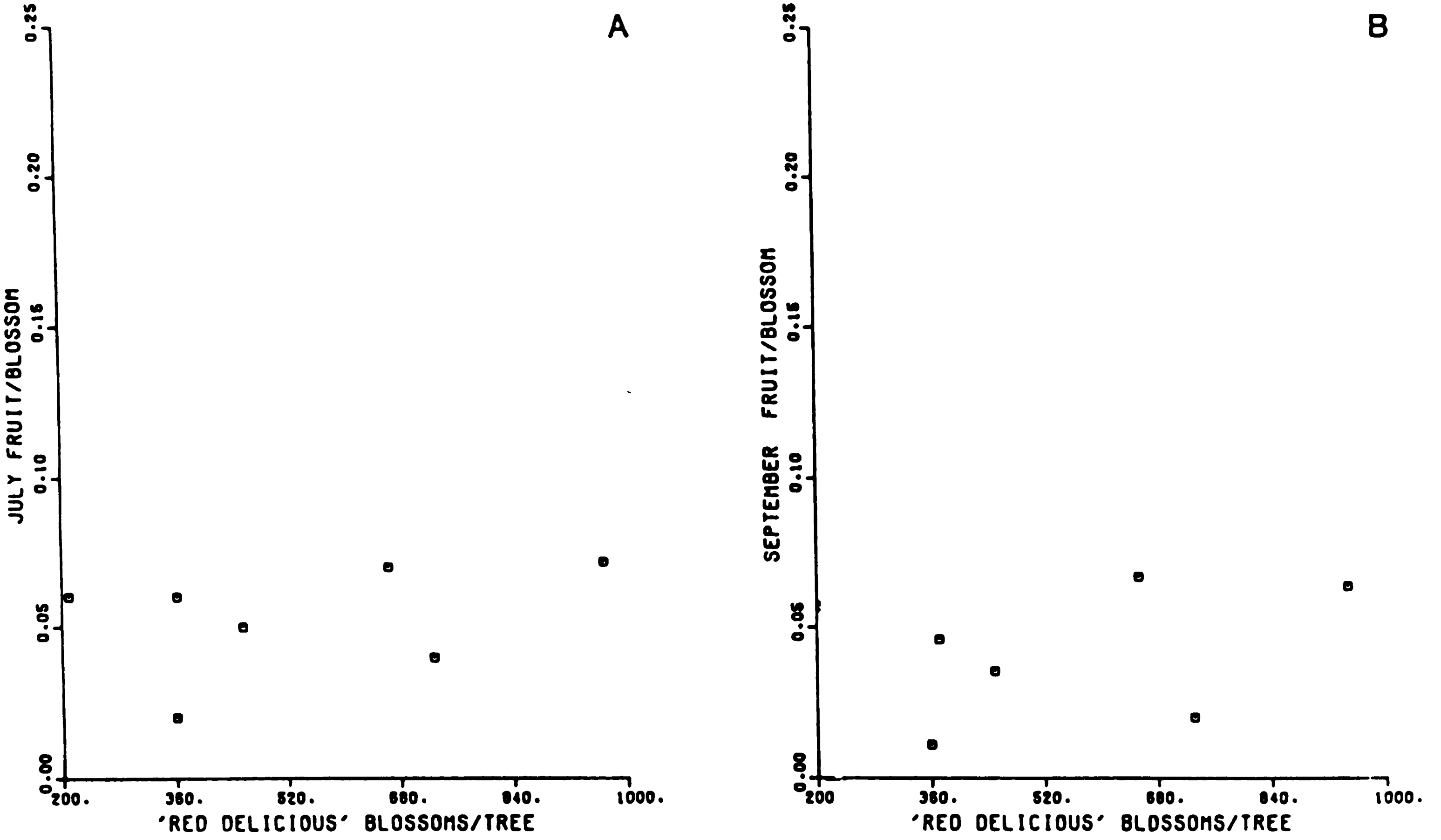


Figure 25. Flowering to Fruiting Percentages as a Function of Blossom Density on 'Delicious' Trees (Ashby's Orchard Site) (A=July Fruiting Percentages, B=September Fruiting Percentages).

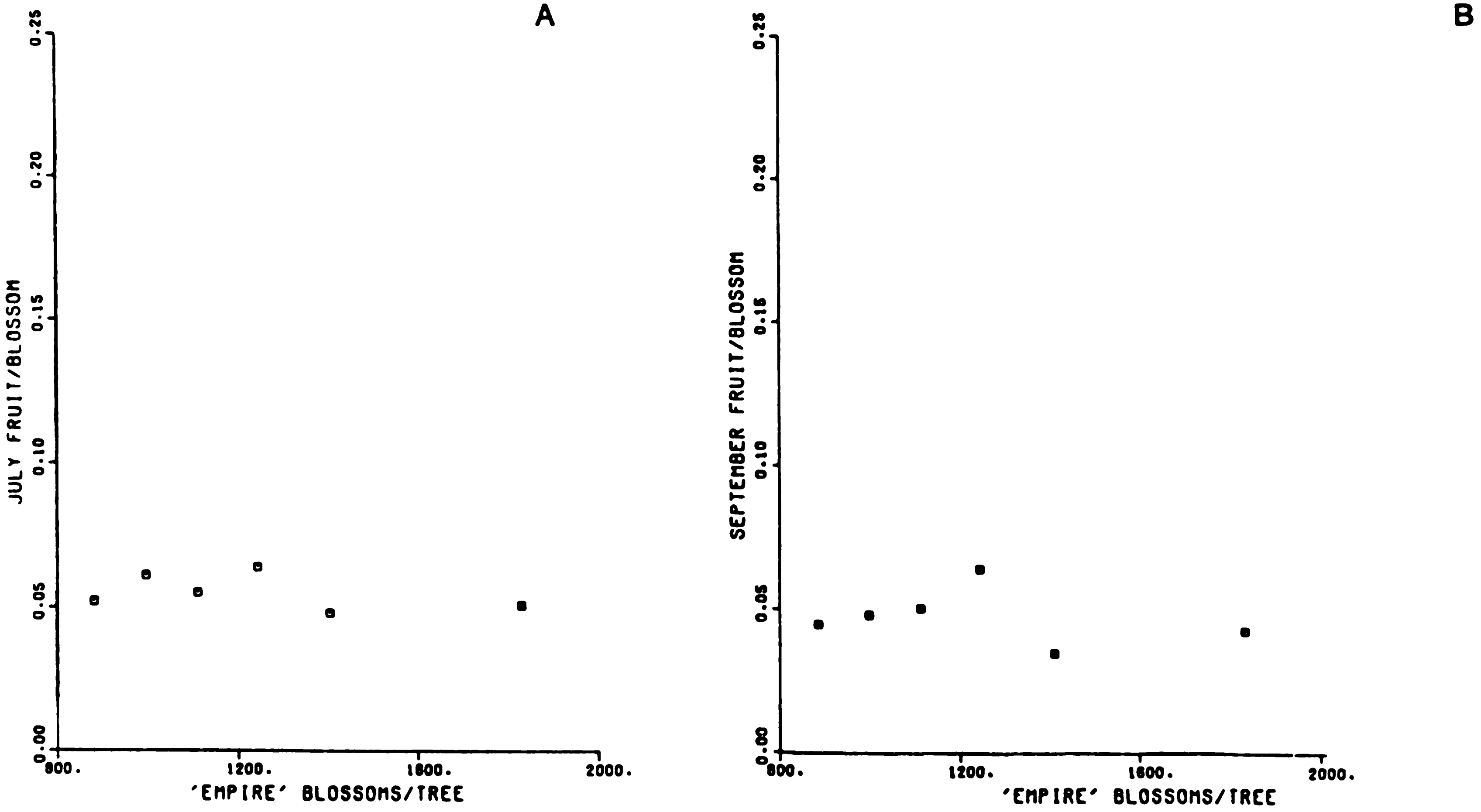


Figure 26. Flowering to Fruiting Percentages as a Function of Blossom Density on 'Empire' Trees. (A=July Fruiting Percentages, B=September Fruiting Percentages).

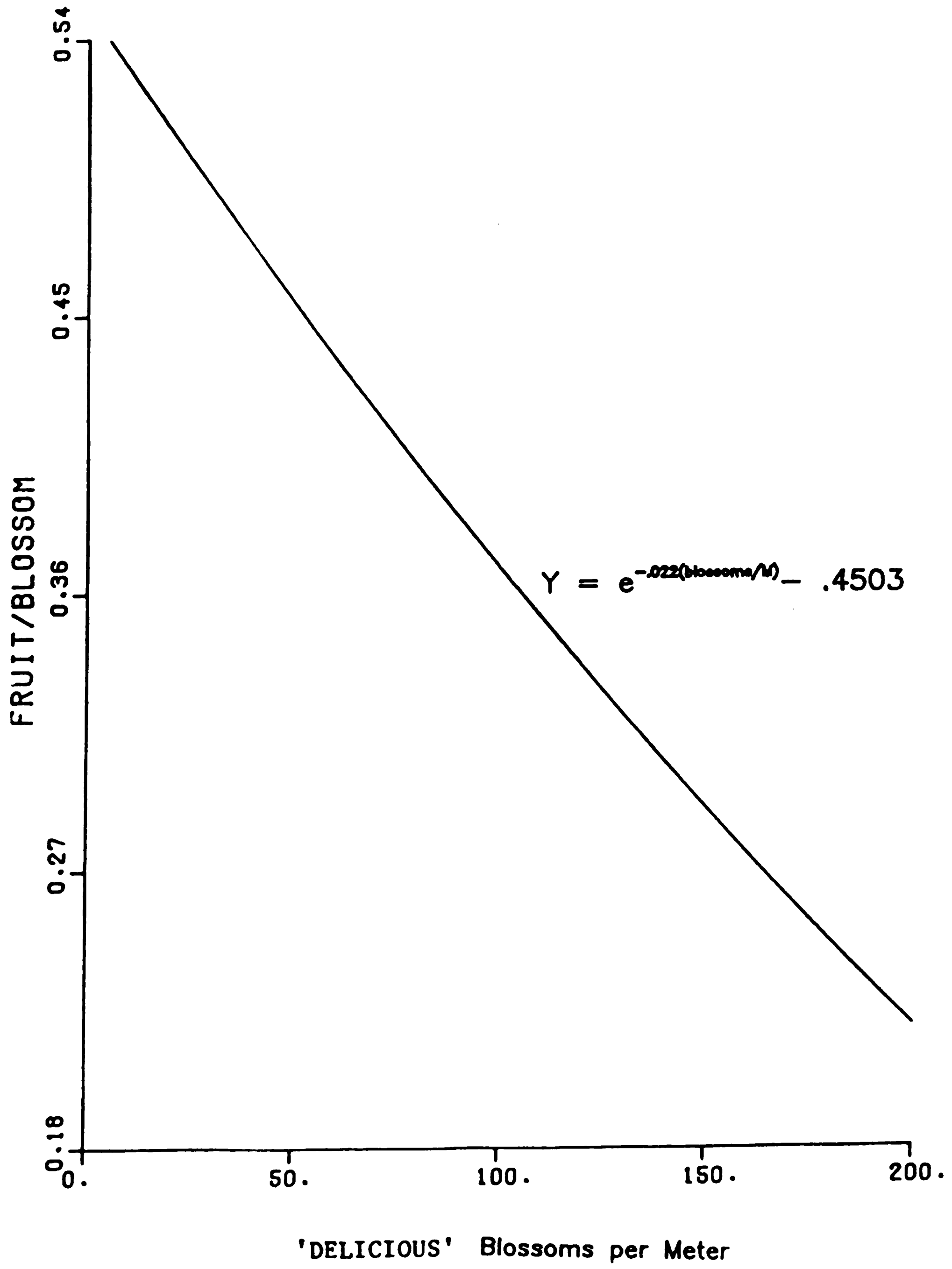


Figure 27. Ideal Initial Fruit Set (i.e., Fruit Set Goal) Based Upon Blossom Density for 'Delicious'.

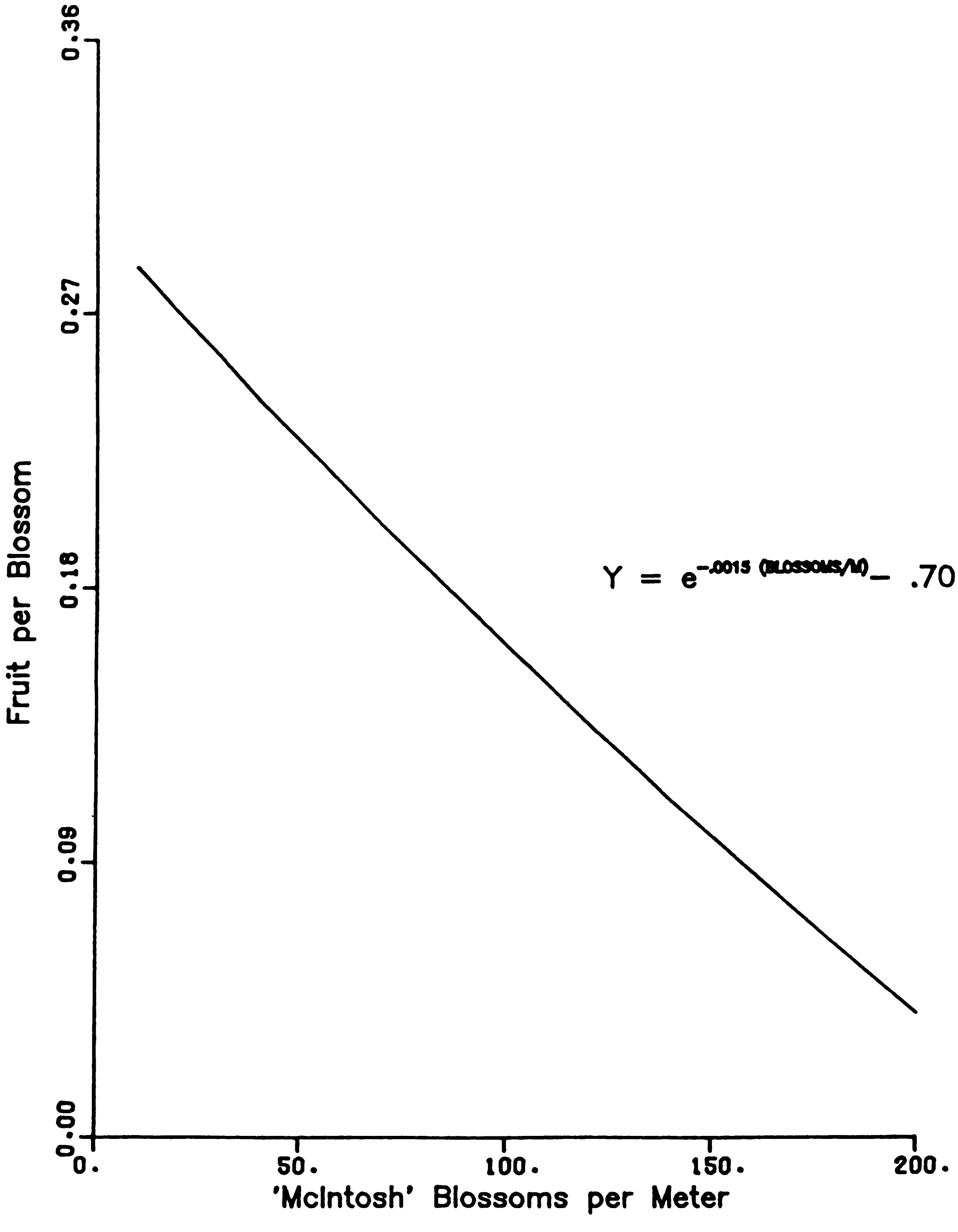


Figure 28. Ideal Initial Fruit Set (i.e., Fruit Set Goal) Based Upon Blossom Density for 'McIntosh'.

Effect of Distance from the Pollinizer on Fruit Set

In 1982 the percentage of blossoms initially setting fruit at Herman's Orchard (in Sutton's Bay) did not differ significantly with respect to distance from the pollinizer ('McIntosh') (Table 4). Initial percentages of blossoms setting fruit ranged between 12.9% (3 rows away, west side of the pollinizer) and 17.9% (next to the west side of the pollinizer).

Seed number per fruit (initial set) was also counted at Herman's in 1982 and analyzed for differences with respect to distance from the pollinizer ('McIntosh') (Table 5). Only trees adjacent to the east side of the pollinizer had significantly more seeds than trees in other rows. Seeds per fruit ranged between 3.70 (three rows away, east side of the pollinizer) and 6.89 seeds per fruit (next to the east side of the pollinizer).

Seed Number on Retained and Abscissed Fruit

Seed number was not significantly different in retained and abcised 'Delicious' fruit at the MSU Horticulture Farm in 1982 (Table 6). Apples retained on the tree averaged 6.41 seeds/fruit, while those abscised during 'June drop' averaged 6.23 seeds/fruit. The Macspur 'McIntosh' trees at this site, though did have a significantly greater number of seeds in retained versus abscised fruit. Retained 'McIntosh' fruit averaged 6.63 seeds while dropped fruit averaged 4.56 seeds. The 'Empire' variety at the MSU Horticulture Farm also had a significantly larger number of seeds in retained (8.28 Seeds/fruit) versus abscised fruit (6.95 seeds/fruit). Seed number in retained 'Empire' apples was also significantly greater than in retained 'McIntosh' or 'Delicious' fruit at this site.

At Herman's Orchard where 'Delicious' trees were arranged in a near solid block design, a significantly greater number of seeds were contained in retained

TABLE 4

Percent of flowers becomming fruit on 'Red Delicious' trees various distances from the pollinizer.*

Rows from Pollinizer	Direction	N	Mean % of flowers becoming fruit ± SD
4 Away	E	8	.167 ± .079a
3 Away	E	8	.167 + .761 a
3 Away	W	8	.129 ± .037 a
2 Away	E	8	.175 ± .023 a
2 Away	W	8	.165 ± .034 a
1 Away	E	8	.163 ± .081 a
1 Away	W	8	.136 ± .058 a
Next To	E	8	.148 ± .042 a
Next To	W	8	.179 ± .057 a

Means followed by the same letter are not significantly different at the 5% level as determined by the F-test.

*Pollinizer ='McIntosh'

TABLE-5

Number of seeds per fruit on 'Red Delicious' Trees Various Distances from the Pollinizer*

Rows from Pollinizer	Direction	N	Mean number of seeds per fruit ± SD.
4 Away	E	20	4.75 ± 1.77 a
3 Away	E	20	3.70 ± 1.89 a
3 Away	W	20	3.90 ± 1.86 a
2 Away	E	20	3.80 ± 2.12 a
2 Away	W	20	4.05 ± 1.73 a
1 Away	E	19	4.53 ± 2.20 a
1 Away	W	20	4.90 ± 2.17 a
Next to	E	19	6.89 ± 3.20 b
Next to	W	20	5.30 ± 2.62 a

Means followed by the same letter are not significantly different at the 5% level as determined by Tukey's W method.

TABLE-6

Seed number on retained and abscissed fruit collected from 1982 orchard sites.

Site	Variety	Sample Size	Average number of retained seeds/fruit ± Standard Error	Sample Size	Average number of seeds/abscised fruit ± Standard Error
MSU Horticulture Farm	Millerspur 'Red Delicious'	64	6.41 ± .275 a	64	6.23 ± .285 a
	Macspur 'McIntosh'	64	6.63 ± .345 a	64	4.56 ± .361 b
	Empire	64	8.28 ± .174 c	64	6.95 ± .217 a
Herman's Orchard	Stark Double Red 'Red Delicious'	32	5.69 ± .302 a	32	3.59 ± .283 b
	Macspur 'McIntosh'	32	8.78 ± .297 c	32	7.91 ± .313 c
Stanek and Son's Orchard	Red Chief 'Red Delicious'	32	7.09 ± .343 a	32	5.84 ± .376
	Macspur 'McIntosh'	32	7.63 ± .276 a	32	7.28 ± .292 a
Ashby's Orchard	Red Chief 'Red Delicious'	32	5.75 ± .262 a	32	5.88 ± .325 a
	Empire	32	8.00 ± .297 a	32	7.97 ± .309 a

Means followed by the same letter at that orchard site are not significantly different at the 5% level as determined by Fisher's LSD.

(5.69 seeds/fruit) as opposed to dropped fruit (3.59 seeds/fruit) (Table 6). 'McIntosh' trees at this site though, did not have significantly more seeds in retained fruit. Apples held on 'McIntosh' trees averaged 8.78 seeds/fruit while dropped fruit averaged 7.91 seeds. At this site, 'McIntosh' fruit had a significantly greater number of seeds in both retained and abscised fruit compared to the number of seeds in retained 'Delicious' fruit.

At Stanek and Sons' orchard, 'Delicious' fruit retained on the trees did not have a significantly greater number of seeds per fruit than those that were abscised (Table 6). Retained fruit averaged 7.09 seeds while abscised fruit averaged 5.84 seeds. 'McIntosh' fruit at this site also did not differ significantly in the number of seeds in retained versus dropped fruit (7.63 seeds/fruit and 7.28 seeds/fruit respectively). In this orchard no significant differences in seed number existed between retained 'Delicious' and 'McIntosh' fruit.

At Ashby's orchard seed number in retained 'Delicious' fruit did not differ significantly from fruit that was dropped. 'Delicious' apples on the tree averaged 5.78 seeds/fruit while those abscised averaged 5.88 seeds/fruit. Retained Empire fruit also did not differ significantly in seed number from those that were abscised. Retained 'Empire' apples contained 8.00 seeds/fruit while those abscised contained 7.97 seeds/fruit. At this site 'Empire' fruit, both retained on the tree and abscised, had significantly more seeds than 'Delicious' apples held on the trees.

DISCUSSION

The system flow diagram used to define the interactions leading to cross pollination and fruit set is shown in Figure 29. Weather factors (temperature,

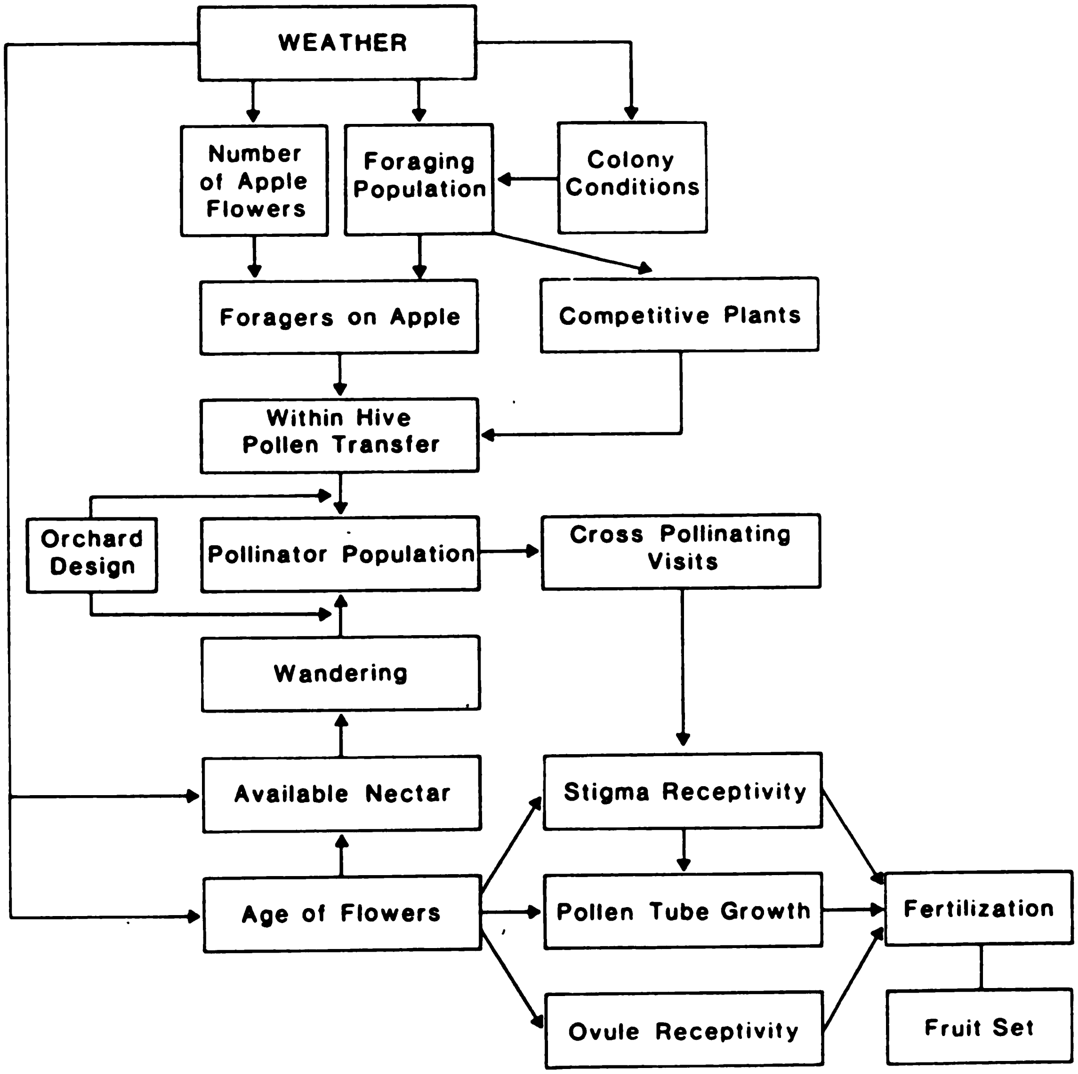


Figure 29. Flow diagram of the components considered in the pollination and fruit set model for 'Delicious' apples.

wind, solar radiation, and rain) are perceived to be the major stimuli to the system because they influence the size of the foraging population, colony conditions, number and quality of blossoms, and nectar availability. Although the state of the bloom affects the size of the foraging population on apple which ultimately influences the rate of fruit set, this is actually a secondary response. The size of the foraging population is first related to weather conditions; the portion foraging apple is then a function of state of bloom.

Although regression equations indicated that there was a high degree of correlation between weather (temperature, wind, and solar radiation), bloom state, and honey bee foraging on apple, the low predictive capabilities of the equations implied that the relationship among these variables is neither additive nor linear. The foraging response to weather and bloom variables was indeed multiplicative, and only one response curve (wind) was found to have a linear relationship with flight activity.

Several authors have found that the relationship between flight activity and solar radiation just before, during, and immediately after the sun's zenith could not be explained using the response equations derived from other hours of the day (Lundie 1925, Wellington 1957, Frisch 1965 cited by Burrill and Dietz 1981, Gary 1975, and Burrill and Dietz 1981). Our attempts at defining the foraging response to solar radiation when the sun is at its zenith also indicated that the response was more random and indeed less predictable during this period (probably from difficulty in honey bee orientation to the sun at this time) even when temperature, wind, and state of bloom were considered.

In the program, the progression of bloom and rate of blossom aging are predicted using accumulated degree days. An analysis of field data indicated that the degree day base for Macspur 'McIntosh' was lower than 'Delicious'. This could explain why 'McIntosh' always blooms before 'Delicious'. Whether varieties blooming after 'Delicious', such as 'Golden Delicious' and 'Northern Spy' have higher threshold tempertures for the expression of bloom could be the subject of further studies. Certainly the degree day base for 'Delicious' and 'Macspur' McIntosh require at least another year of validation and fine tuning, but if the method used to predict base temperature for 'McIntosh' and 'Delicious' is indeed valid, it could be used to define bloom threshold temperatures for other varieties.

While collecting data to define the progression of bloom, areas of future model sensitivity became apparent. Currently there is no incorporation of the effects of wind and rain on petal retention and attractiveness of bloom. Blossoms have reduced petal retention as they age (and probably after being cross pollinated), and petal fall can be expediated by strong rains or high winds. Because honey bees rely upon petals for direction to the nectaries, the bloom may lose its attractiveness prematurely under these conditions. If blossoms depetaled by wind or rain cease to be attractive and rewarding then the influence of these weather factors on the size of the apple forager population will have to be considered.

Predictions on the size of the apple foraging population are based upon three factors: 1) the number of colonies introduced/hectare, 2) the state of the apple bloom, and 3) the weather. Field data indicated that apple bloom is fairly attractive even during king bloom, and by peak bloom may attract almost 50% of the foraging population. The foraging population response to state of bloom was different though for 'Delicious' and 'McIntosh'. This may have occurred because these varieties were planted near each other, and had overlapping bloom periods which may have caused their foraging populations to interact. 'McIntosh' blooms before 'Delicious', and prior to its peak bloom was always more attractive than the 'Delicious'. Conversely, after the 'McIntosh' peak bloom the foraging population began to decline earlier than in 'Delicious', because at that time the 'Delicious' trees had more blossoms and were possibly attracting bees from the 'McIntosh'. Hence foraging activity on 'McIntosh' after peak bloom declined more rapidly than on the 'Delicious'. Consequently, separate curves for each variety were required to describe the foraging response to state of bloom.

From the onset of the model's development, the source of honey bees foraging apple and carrying compatible pollen (that could hence initiate fruit set) was seen to be a pivotal point in making accurate fruit set predictions. Results from field data indicated that distance from the pollinizer had no effect on the percentage of 'Delicious' flowers that set fruit in the years and orchards in which this study was conducted (Table 4). If competition for nectar existed, and prompted honey bees to leave a tree and visit another, the nearest tree would most likely be the next one foraged. Observations of honey bees working apple blossoms showed that a majority of bees that left a tree visited others in the same row, and crossing between rows was an infrequent event, especially in orchards with standard size trees (Free 1960). This behavior should have resulted in a decrease in fruit set with distance from the pollinizer, as previously reported to sometimes occur in fruit trees (Williams 1959, Free 1962, Spencer-Booth 1964b), but our field data did not support this hypothesis. Furthermore, honey bees foraging 'Delicious' and 'McIntosh' trees were found to be carrying pollen from varieties and species that on some occasions was located several hundred meters away from where the honey bee was captured. Honey bees probably would not show a caloric profit with foraging areas as large as indicated by the pollen types on their bodies, and a single tree probably has enough nectar to satiate many bees. Still every forager examined in our experiment was carrying several types of pollen, which makes the idea of pollen acquisition in the hive appear to be a possible explanation.

If in hive pollen transfer is creating a large part of the pollinator population, orchard design and choice of pollinizer variety could have a profound influence on the fruit set rate. If the pollinizer variety blooms after 'Delicious' and colonies are introduced when the 'Delicious' first blooms, the majority of apple pollen in the hive would be 'Delicious'. Consequently, pollinizer pollen could be significantly diluted throughout the period prior to 'Delicious' peak bloom, and hence reduce the effectiveness of the pollinator population in terms of their ability to cross pollinate 'Delicious' king blossoms with pollen acquired in the hive. Whether blossoms can still set fruit if their stigmata are first coated with self-or non-apple pollen and then later cross pollinated is a question that requires further experimentation.

The ratio of pollinizer to 'Delicious' trees could also influence the pollinator population created by in-hive pollen transfer. If 'Delicious' trees are planted in near solid block arrangements and pollinizer trees are greatly outnumbered, compatible pollen could be diluted and again possibly reduce the effectiveness of the pollinator population. On the other hand solid block arrangements of 'Delicious' could possibly produce good fruit set if a pollinizer block (that blooms before 'Delicious') is located nearby, and has honey bee colonies located within it.

The effectiveness of in hive pollen transfer may have other constraints in addition to the ratio of pollinizer/'Delicious' trees. It is possible that a certain foraging population level must be obtained in a colony before sufficient contact among nest mates occurs prompting an effective mixing of pollen. A minimum time of uninterrupted foraging may also be necessary to achieve maximum pollen exchange between nest mates. Finally, the distribution of the foraging population on apple and competitive plant species undoubtedly influences the effectiveness of in hive pollen transfer in the creation of a pollinator population. If a majority of foragers are working competitive plants, this type of pollen would predominate in the hive and possibly on the body's of apple foragers. This could explain cases where some apple stigmata examined in this study had relatively high percentages of yellow rocket and other competitive plant pollens.

The influence of available compatible pollen on fruit set and retention could possibly explain the differences in seed number on retained and abscised fruit at the various orchard sites. When 'Delicious' or 'McIntosh' trees were planted in solid blocks ('McIntosh' at the MSU Horticulture Farm and 'Delicious' at Herman's), there were significantly fewer seeds in fruit abscised during 'June drop' than in those retained on the tree. Trees planted with an excess of unrelated varieties nearby did not show this difference ('Delicious' and 'McIntosh' at the MSU Horticulture Farm and Stanek and Sons' Orchards). The only exception was in 'Empire' trees at the MSU Horticulture Farm which contained significantly fewer seeds in abscised versus retained fruit, although they were not planted in solid block arrangements. This difference in seed number was not repeated in the 'Empire' trees at Ashby's orchard though.

If compatible pollen is limited or greatly diluted, seed number may become a significant constraint on fruit retention. It is possible that if sufficient amounts of compatible pollen exists, and seed number among fruits is essentially equivalent, other factors (spur location and vigor, degree of apical dominance in the variety, fruiting the previous year, fruit to leaf ratio etc.) may have a stronger influence on fruit retention. On the other hand, if compatible pollen is limited and fruits differ significantly in their seed number, this factor may have an influence on fruit retention.

Field data indicated that the transfer of compatible pollen was really not a constraint on fruit set in the years and orchards in which this study was conducted. If this is true, flower quality (in terms of a blossom's probability of setting fruit if cross pollinated) may be the most important limiting factor in fruit set. Currently flower quality (in terms of number of of receptive ovules) is expressed as a function of time of opening in the bloom period and accumulated degree days since anthesis. Updates on ovule receptivity are based on the findings of Hartman and Howlett (1954) concerning ovule degeneration with time, although their study did not specifically relate ovule receptivity with the degree day interval when blossoms opened, blossom age in degree days, or flowering spur position on the branch.

Additional experiments will be needed to validate the rate of ovule degeneration with accumulated degree days for both 'Delicious' and pollinizer varieties, but to truely define the state of flower quality, additional parameters may be needed in the model. For example, ovule longevity has been associated with tree vigor and available nutrients, but the model does not yet have sensitivity to these factors (Williams 1965). Currently blossom viability, determined by samples taken at "tight cluster" stage, is the only factor concerning flower quality considered in the model that is specific to a site.

Because results of our experiments indicated that the pollinator population (i.e. honey bees carrying compatible pollen) can be quite large, and may not be the severe constraint on fruit set as once supposed, incorporation of parameters that can more accurately update blossom quality will certainly be a high priority area of future research and model elaboration.

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IDENTIFYING FACTORS THAT INFLUENCE FRUIT SET IN 'DELICIOUS' APPLES USING REDAPOL SIMULATIONS

INTRODUCTION

As simulation modeling has advanced the study of plant-pest relationships, so it can increase the understanding of plant-pollinator relationships which culminate in fruit set. A systems approach could predict fruit set by combining predictions on cross pollination rates with updates on flower quality (in terms of probability of setting fruit if cross pollinated). In addition to their use by growers, fruit set models are excellent research tools because they allow experimentation on fruit set parameter combinations that would be difficult or costly to duplicate in the field. Furthermore, variation from site to site or year to year that exists in field results could be eliminated using simulation models. With this in mind, a pollination and fruit set model (REDAPOL) was constructed for 'Delicious' apples.

In the 'Delicious' fruit set system, several parameters were suspected to strongly influence fruit set predictions. Orchard design, in terms of the ratio, size, and arrangement of 'Delicious' and pollinizer trees, was one such parameter. If availability of compatible pollen is limited because 'Delicious' blossoms far outnumber those of the pollinizer, fruit set may be limited even if flight weather is good and blossom quality is high. It is possible under these circumstances that compatible pollen becomes so diluted that its presence on the stigma is either rare or at so low a level, it is ineffective in setting fruit. To test this assumption in the field, several different orchard designs would be needed. However, even after statistical analysis the results would reflect some conditions existing at a site that would be difficult to standardize (tree vigor, previous fruiting history, tree age, rootstock, soil type, irrigation practices and size of the honey bee population), so that the influence of orchard design alone would be difficult to assess. This problem could be eliminated by analyzing orchard designs using REDAPOL.

Another variable that most likely influences fruit set is the number of honey bee colonies introduced per hectare. The ideal colony number is undoubtedly specific for a particular orchard design and set of weather conditions. Consequently, a blanket recommendation for the number of colonies required per hectare to insure a commercial fruit set is not possible because the number is not a constant, but a variable. Predictions on fruit set rates under different colony/hectare densities, could be made for various orchard designs, and weather conditions using REDAPOL, and hence direct colony rental decisions.

In addition to predicting the number of colonies required for a commercial fruit set, the time during bloom when honey bee colonies should be removed could also be predicted with a pollination and fruit set model. If a fruit set goal, based on blossom density is established at the beginning of the simulation, daily fruit set predictions could report when that goal has been achieved. This could prevent overset and the need for thinning sprays.

The conditions under which honey bees acquire compatible pollen and initiate fruit set can possibly be defined using a pollination and fruit set model. Currently there are two hypotheses used to explain a honey bee's acquisition of compatible pollen. The first involves competition for nectar which forces some bees to move from tree to tree to acquire a full nectar load (Butler 1944). If the honey bee happens to move from a pollinizer to a 'Delicious' tree, she will cross pollinate blossoms. This hypothesis can be tested with REDAPOL because competition for nectar and honey bee movement can be simulated, and hence the size of the resulting pollinator population (i.e., honeybees carrying compatible pollen) can be estimated along with its contribution to fruit set.

Another possible source of pollinators could be from contact among nest mates in the hive, which results in the transfer of compatible pollen (Karmo and Vickery 1954). Although not much is known about the constraints on "in hive pollen transfer," some reasonable assumptions can be made in order to construct a simulation of this event. For instance, the percentage of the total foraging population leaving the hive the previous hour undoubtedly affects the quantity of pollen coming into the hive and the probability of pollen exchange between nest mates. The percentage of the foraging force on 'Delicious,' pollinizer, and competitive plants probably also influences the size of the pollinator population arising from in-hive pollen transfer, because it dictates the percentage of pollen types entering the hive. REDAPOL simulations could help define the size on the pollinator population arising from in-hive pollen transfer, and evaluate its contribution to fruit set.

Flower quality, in terms of ovule receptivity, may also influence the rate of fruit set during bloom. After anthesis, 'Delicious' blossoms have a probability of setting fruit that decreases continuously as the open blossom ages. Hartman and Howlett (1954) reported a linear decrease in fruit set if pollination was delayed from 1 to 48 hours after anthesis, with the lowest values at 72 hours and thereafter. Although previous reports on ovule degeneration have been expressed in chronological time, accumulated degree days may indeed be a better parameter on which to predict a blossom's fruit set potential. The influence of temperature on flowering is self-evident in its effects on bloom length. Apple bloom can last up to 14 days if the weather is cool, but can be reduced to 5-7 days if temperatures are high. Decreasing probabilities of fruit set with blossom aging can be simulated using REDAPOL, and hence be used to evaluate flower quality's influence on the fruit set rate.

REDAPOL was developed because fruit set models can serve as both research tools and integral parts of overall crop management programs. Simulations were run using REDAPOL to test the influence of orchard design, weather, colonies/hectare, flower viability, and rate of blossom aging on the fruit set rate. The source of the honey bee population responsible for cross pollination (i.e., movement from tree to tree or in-hive pollen transfer) was also examined using simulations.

MATERIALS AND METHODS

Initialization of Orchard Parameters

In the model's initialization subroutine, various orchard characteristics are required to set the stage for fruit set predictions. They include orchard size, tree height, width, trunk height (from ground to first main limb), and number of flowering spurs per meter of branch. The average number of blossoms per tree and the ideal fruit set percentage (fruit/blossom* 100%) is then calculated from this information. Additional input is required about the arrangement of 'Delicious' and pollinizer rows so that the orchard design's influence on fruit set can be analyzed. Required input for this includes the distance between trees in a row and between rows, the number of rows in the 'Delicious'/pollinizer pattern, the number of solid 'Delicious' rows in the pattern, and the percentage of pollinizer trees in the rows containing pollinizers. The user is also asked to sample the orchard for the percentage of viable blossoms in each variety. Finally, the first day of bloom and the number of colonies that will be introduced (and their date and time of introduction) must be specified.

The same orchard design and parameters were used in simulations to test the effects of weather, tree size, flower quality, colony/hectare density, and source of the pollinator population on fruit set. The orchard was composed of 'Delicious' trees (4.0m high, 2.5m wide with 0.5m of trunk) and 'McIntosh' pollinizer (5.0m high, 3.0m wide, with 0.5m of trunk) arranged in a pattern where three rows of 'Delicious' were followed by three rows of 'McIntosh.' Trees were spaced 6.1m apart between rows and 4.6m apart within a row. 'Delicious' trees averaged 25 flowering spurs/m of branch while 'McIntosh' averaged 30. Flower viability at anthesis averaged 90% for both varieties. Unless otherwise noted, colonies were introduced at a density of 2.5/hectare (1 colony/acre).

Construction of Weather Tapes

When REDAPOL is used for predictions of actual fruit set rates, weather is input from data collected by a Campbell Instrument CR-21 micrologger.* Temperature, relative humidity, wind speed, and solar radiation sensors are required. For the purpose of simulating the influence of various weather scenarios on fruit set though, weather tapes were assembled so that they would contain specific conditions. The tapes were constructed by inputting a single day's weather and then duplicating it (unless otherwise specified) for the entire bloom period.

In order to compare differences in fruit set rates when weather conditions deviate from the optimum, an 'ideal flight weather' tape was constructed. This tape contains eleven hours of optimum flight weather each day during bloom

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*Campbell Scientific Inc., P.O. Box 551, Logan, Utah 84321.

(800-1900 hrs.) with temperatures ranging between 21°-31°C, calm winds, and no cloud cover. The 'good flight weather' tape contains conditions that will cause a reduced level of foraging compared to the tape of 'ideal flight weather.' The 'good flight weather' tape contains daylight temperatures between 10°-16°C, winds between 21-26 km/hr, and slightly overcast skies (i.e., solar radiation values between 19-30 microamps/1000 watts/m^{-2}).

To examine the influence of rain and interruptions in flight, weather tapes were constructed which contain periodic rain storms. Under the conditions of a tape named 'warm rain,' each day has only three hours of flight weather which occur between 1200-1400 hrs. During the day temperatures range between 9°-31°C with the highest temperatures occurring during the flight interval. Wind speeds during the non-rain period range between 11-14 km/hr, and the skies are almost clear (i.e., solar radiation values are between 27-39 microamps/1000 watts/m^{-2}).

Finally, a tape was constructed to examine the amount of fruit that would set if flight weather was restricted (due to rain) to one day during bloom. Several of these tapes were assembled differing only in the day during bloom when flight weather occurs. On the day of flight, ideal conditions were programmed to exist, while on the rainy days temperatures were set high enough so the bloom would continue to age (i.e., temperatures are always higher than 5°C) even though flight weather did not exist. With this tape, the maximum amount of fruit that can be set on a single day during bloom could be discerned.

Assumptions and Framework of the Model

REDAPOL's fruit set predictions are based upon updates on the honey bee population in a potential cross-pollinating state, and blossoms whose age and probabilities of fruit set have likewise been updated. REDAPOL was designed to run on two discrete time systems: physiological (accumulated degree day; DD) and chronological time. State of bloom, forager population size, number of cross-pollinating visits and accumulated fruit set are updated hourly. The actual number of open blossoms and their probabilities of fruit set if cross pollinated are updated using state equations which have accumulated degree days as their time element. Based upon field data, the threshold temperature for the progression of 'Delicious' bloom is 5°C while for 'McIntosh' it is 1°C.

In REDAPOL the probabilities of cross pollination leading to fruit set are updated in two dimensions. The first involves the blossoms period of opening during bloom (i.e., king blossom, early lateral, later laterals). The second addresses the number of degree days that have accumulated since the blossom's day of anthesis. Based upon reports that king bloom is composed of the highest quality blossoms, and laterals have a relatively lower potential fruit set especially if the king blossom sets fruit (Detjen 1929); the probabilities of fruit set on the day of anthesis are greatest for king blossoms. The probability of cross pollination leading to fruit set then declines as the number of accumulated degree days since anthesis increases. This is based on reports of reduced fruit set rates in blossoms where cross pollination is delayed for 48 hrs or more after anthesis (Hartman and Howlett 1954). Based on these assumptions then, the fruit set rate is always highest during the early part of bloom.

Another group of assumptions used in the construction of REDAPOL relates to the source of honey bees with cross pollinating potential (pollinators). In the model, pollinators occur from two sets of conditions. The first involves competition for nectar, which forces honey bees to move from tree to tree to acquire a full nectar load (Butler 1944). If movement occurs between trees of unrelated varieties, cross pollination is predicted to occur. REDAPOL is programmed so that the direction honey bees move when leaving a tree is a function of distance to the next tree. As distance between trees increases, the probability of a honey bee moving that distance decreases. This assumption is based on the conservative nature of honey bee movement in apple orchards. Honey bees have been reported to generally remain on the same tree for much, if not all, of a foraging trip, and when movement occurs, it is most likely to the next tree in a row. Movement between rows is a less frequent event in both standard and dwarf tree plantings (Free and Spencer-Booth 1964 a,b; Free 1966).

An additional means of acquiring compatible pollen is through its transfer among honey bees in the hive (Karmo and Vickery 1954). Our field data has indicated in-hive pollen transfer may indeed be making a large contribution to the pollinator population. This conclusion was drawn from data which indicated that honey bees were working apple blossoms while carrying pollen from several apple varieties (and in some cases, other plant species). Although constraints on this pollinator source have not been documented in the field, in order to simulate in-hive pollen transfer and predict its contribution to fruit set, the following relationships were assumed:

1) In-hive pollen transfer increases logarithmically with the size of the foraging population.
2) In-hive transfer of viable pollen does not occur unless there is at least two hours of continuous flight.
3) Apple foragers (and perhaps foragers of other plant species) can leave the hive with enough compatible pollen to cross-pollinate a varying percentage of blossoms.

4) The number of blossoms an apple forager can cross-pollinate with in-hive pollen is lower during the hours of peak pollen dehiscence (900-1300 hrs) than at other times of the day.

5) Pollen in the hive loses its viability overnight.

When the number of cross pollinating visits from tree to tree movement and in-hive pollen transfer are totaled for the hour, the visits are distributed to open blossoms. Estimates of fruit set are then made by multiplying the probability of fruit set for each blossom age group by the number of blossoms in that group that have received a cross pollinating visit. Because pollen grains must germinate and grow down the style before fertilization can occur, a delay of 30 DD_5 for 'Delicious' and 40 DD_1 for 'McIntosh' is assumed between cross pollination and fruit set (i.e., fertilization is assumed to occur 48 hrs after cross pollination if temperatures average 21^oC). Consequently, the number of receptive ovules that exist at the time when pollen tubes have entered the ovary is the point from which fruit set probabilities are calculated. It is assumed that an ovary must have at least 4 fertilized ovules (i.e., seeds) to set a fruit of desirable size.

RESULTS

The Influence of Orchard Design of Fruit Set

In this analysis two general types of orchard designs were examined for their influence on fruit set. The first is a pattern where one pollinizer row is separated from the next by several rows of 'Delicious.' Plantings in our analysis ranged from alternating pollinizer and 'Delicious' rows, to a pollinizer row followed by five rows of 'Delicious.' In these plantings, average 'Delicious' fruit set decreased as the number of trees between two pollinizer rows increased (Table 1).

Forty-three percent of the 'Delicious' blossoms set fruit by the end of bloom for an every other row 'Delicious'/pollinizer arrangement, while 22.9% fruit set was predicted for a one pollinizer/five 'Delicious' arrangement. These fruit set predictions are based upon 'ideal flight weather' in an orchard of semi-dwarf trees (2.44m 'Delicious' and 3.05m 'McIntosh'). Based upon blossom density on the 'Delicious' trees, the ideal commercial fruit set goal of 14.8% (i.e., 14.8% of the blossoms should set fruit) was met during the second day of bloom in all of these plantings under the described conditions.

A second set of orchard designs contained variations of a one-to-one ratio of 'Delicious' and pollinizer trees. Comparisons were made between plantings of alternate rows of both varieties, and increasingly larger blocks of 'Delicious' and pollinizer trees still at a one-to-one ratio. Fruit set did not decrease significantly under 'ideal flight weather' conditions as blocks of 'Delicious' increased (50.01-47.2%, Table 1), and the 'Delicious' fruit set goal (14.8%) was met in all cases on the second day of 'Delicious' bloom.

In contrast, 'McIntosh' set was considerably lower than the 'Delicious' when planted in a one-to-one ratio no matter what the pattern. 'McIntosh' fruit set increased though, as the ratio of 'Delicious' to 'McIntosh' increased. When 'McIntosh' trees were outnumbered by 'Delicious,' 'McIntosh' trees were predicted to overset and would have required thinning.

The Influence of the 'Wandering Honey Bee' Population on Fruit Set

In the version of REDAPOL used in these simulations, the fruit set by honey bees moving from pollinizer to 'Delicious' trees was recorded separately

Table 1

The influence of orchard design on fruit set. *

Orchard Design	Petal Fall Fruit Set (Fruit /Blossom * 100) 'Delicious'	'McIntosh'	Fruit Set Relative to Alternate Row Planting (Fruit Set/Alternate Row Fruit Set) * 100 'Delicious'	'McIntosh'
xxx oxo xxx	13.9	51.3	27.8	766
xoxo	50.0	6.7	100	100
xxxo	25.6	20.6	51.2	308
xxxxo	26.2	34.9	52.4	521
xxxxxo	22.9	42.2	45.8	630
xxoo	48.4	6.8	96.8	101
xxxooo	47.9	6.9	95.8	103
xxxxoooo	47.7	6.9	95.4	103
xxxxxooooo	47.5	6.9	95.0	103
xxxxxxoooooo	47.4	6.9	94.8	103
xxxxxxxooooooo	47.2	6.9	94.4	103

* Constant parameters in the Simulations
Tree Size: Semi-dwarf
Colony Density: 2.5 colonies/hectare
Weather Tape: Ideal flight weather
x = 'Delicious'
o = 'McIntosh'

from cross pollinations resulting from compatible pollen acquired in the hive. Honey bees were predicted to move from a tree if they repeatedly encountered empty (i.e., nectarless) blossoms. The probability of moving to an unrelated tree was then predicted to be a function of the distance to the unrelated tree versus the distance to the next tree in the same row. In all simulations, trees in the same row were always closer than trees in adjacent rows. The "wandering honey bee" population was updated hourly in the program when flight conditions existed, and essentially its size depended on available rewarding blossoms and the size of the foraging population.

In all orchard designs tested in these simulations the fruit set contribution of wandering honey bees was found to be extremely small (i.e., less than 1%) (Table 2). When RDA trees were planted in equal numbers with the pollinizer, total fruit set ranged between 47.21%-50.01% (i.e., percentage of flowers that set fruit if colonies remained in the orchard until petal fall) (Table 2). In these arrangements, only about 0.01% of the total fruit set was predicted to result from honey bee movement from tree to tree. 'Delicious' fruit set by wandering bees increased when pollinizer rows were spaced between two, three, or four rows of 'Delicious,' or if pollinizers were interplanted in 'Delicious' rows. The range of fruit set percentages resulting from these simulations represented rows closest to (high value) and furthest from (low value) the pollinizer.

In addition, there was limited fruit set contribution by wandering honey bees on the pollinizer trees. The highest amount of fruit set by wanderers occurred when pollinizers were planted as every third tree in every third 'Delicious' row. This planting also resulted in the largest pollinizer total fruiting percentage when compared to all other tree arrangements.

Table 2

Fruit set contribution by wandering honey bees *.

Orchard Design	Petal Fall Fruit Set by wandering Honey Bees (fruit/blossom * 100) 'Delicious'	Petal Fall Fruit Set by wandering Honey Bees (fruit/blossom * 100) 'McIntosh'	Total Petal Fall Fruit Set (fruit/blossom * 100) 'Delicious'	Total Petal Fall Fruit Set (fruit/blossom * 100) 'McIntosh'
xxx oxo xxx	0.07 - 0.17	0.68	13.0	51.3
xo	0.01 - 0.01	0.02	50.0	6.7
xxo	0.02 - 0.02	0.08	31.7	12.6
xxxo	0.02 - 0.07	0.26	25.6	20.6
xxxxo	0.04 - 0.17	0.58	26.2	34.9
xxoo	0.01 - 0.01	0.02	48.4	6.8
xxxooo	0 - 0.01	0 - 0.02	47.9	6.9
xxxxoooo	0 - 0.01	0 - 0.02	47.7	6.9
xxxxxooooo	0 - 0.02	0 - 0.02	47.5	6.9
xxxxxxoooooo	0 - 0.02	0 - 0.02	47.4	6.9

Constant parameters in the simulations:
Tree Size: semi-dwarf
Colony Density: 2.5 colonies/hectare

Weather Tape: Ideal flight weather
x = 'Delicious o = 'McIntosh'

In these simulations the difference between petal fall fruit set by wanderers and total petal fall fruit set was due to cross pollinations by honey bees that acquired compatible pollen in the hive. This source of pollinators was responsible for the majority of cross pollinations, especially in orchard designs that simulated solid block plantings. When 'McIntosh' rows were input between rows of 'Delicious,' the fruit set contribution by wanderers increased but was still quite small in relation to total petal fall fruit set (Table 2).

The Influence of Tree Size on Fruit Set

It has been reported that dwarf and semi-dwarf apple plantings out-produce orchards with standard trees, because smaller trees have more fruiting wood per hectare (McGregor 1976, Westwood 1978). The model was tested for this behavior by inputting trees with standard, semi-dwarf, and dwarf dimensions. Weather ('ideal flight weather' conditions), blossom density per meter of branch, and colonies/hectare were identical for all simulations. Based upon tree size and spacings in the simulations, there were 363 standard trees, 1725 semi-dwarfs, and 2435 dwarf trees per hectare.

Results of the simulations showed that the model did predict that dwarf trees out produce both standard and semi-dwarf plantings (Table 3). The highest 'Delicious' and 'McIntosh' fruit set rate (fruit/blossom) occurred in the orchard of standard trees, even though less fruit was produced (compared to the dwarf plantings). Fruit set in 'McIntosh' did not increase, as it did in the case of 'Delicious,' when semi-dwarf trees were substituted for standard. 'McIntosh' fruit set did increase by 60% though, when simulations were conducted with 'McIntosh' trees on dwarf rootstock.

Table 3. The influence of tree size on fruit set.*

Tree size	Petal Fall Fruit Set (Fruit/Blossom * 100%)		Bushels / Hectare**	
	'Delicious'	'McIntosh'	'Delicious'	'McIntosh'
Standard	41.9	6.1	1877-2502	402-535
Semi-Dwarf	37.2	3.5	2511-3348	402-536
Dwarf	24.8	5.3	3122-4165	670-895

*Constant parameters in the simulation's
Colony Density: 2.5 colonies/hectare
Weather Tape: Ideal flight weather
Orchard Design: xxxooo
x = 'Delicious'
o = 'McIntosh'

**Range of bushels is dependent upon size of apples

The Influence of Weather on Fruit Set

Final fruit set predictions were compared among orchards that differed only in weather conditions during bloom. Weather tapes used in this group of simulations differed greatly from one another in terms of their ability to promote foraging. Under 'ideal flight weather' conditions, the foraging population increased throughout the morning (beginning at 800 hrs) and peaked at 1300 hrs, about 99% of its potential per colony. The foraging population then slowly decreased until 2000 hrs when foraging stopped because of low light intensity.

Under 'good flight weather' conditions the foraging population also continued to increase until 1300 hrs, but at a slower rate than under 'ideal flight weather' conditions. The foraging population peaked (at 1400 hrs) at about 40% of its potential. Under conditions of 'warm rain,' flight was restricted to a three hour period (1300-1500 hrs) each day. During this time, foraging increased during the first two hours as the rainstorm dissapated and then decreased to zero in the third hour as the next rainstorm entered the orchard.

The next set of simulations involved weather tapes that permitted only one day of flight weather during bloom (continuous rain occurred on all other days). Six weather tapes were constructed for these tests. The tapes differed only in the day during 'Delicious' bloom when flight weather occurred. During the day of flight, weather conditions were programmed to be ideal (i.e., they were identical to any one day on the 'ideal flight weather' tape) for this activity.

Based upon blossom density of the 'Delicious' and 'McIntosh' trees, the fruit set goal (i.e., fruit/blossom *100) in all simulations was predicted to be 10.2% and 8.2% respectively. Under conditions of 'ideal flight weather' and 'warm rain,' the 'Delicious' fruit set goal was met at various times during the third day of bloom (approximately 41 DD_5 or 53 DD_1). Under 'good flight weather' conditions the 'Delicious' goal was met on the ninth day of bloom (about 50 DD_5 or 86 DD_1). The optimum fruiting percentage was met on 'McIntosh' trees only under 'ideal flight weather' conditions and then not until the end of bloom (Table 4). As expected, final fruit set on both varieties was highest under 'ideal flight weather' conditions. The lowest final fruit set occurred in 'Delicious' under 'warm rain' conditions, while in 'McIntosh' 'good flight weather' produced the lowest set (Table 4).

When flight weather was restricted to one day during bloom, the highest fruit set values were predicted when flight occurred on the sixth day of 'Delicious' bloom. In this group of simulations, final fruit set percentages for 'Delicious' ranged between 0.19% (flight on day-1 of 'Delicious' bloom; about 0-16DD_5) and 15.15% (flight on day -6 of 'Delicious' bloom; about 75-91 DD_5) (Table 4). 'McIntosh' fruit set ranged between 0.02% (flight on day-2 of 'McIntosh' bloom; about 19-37 DD_1) and 3.85% (day-7 of 'McIntosh' bloom; about 114-132 DD_1) (Table 4).

The Influence of Colony Number and Orchard Design on Fruit Set

Simulations were run with various 'Delicious' and 'McIntosh' tree arrangements to test if fruit set could be increased by introducing additional colonies. Results of these simulations are summarized in Table 5. In all cases fruit set in both varieties was increased by adding more colonies per hectare especially in the 2.5-10 colonies/hectare range. The fruit set goal for 'Delicious' (10.2%) was met in all orchard designs prior to petal fall with 2.5 colonies/hectare. Essentially, the additional colonies were not really necessary then, and the fruit would have required thinning to achieve good size. The maximum petal fall

Table 4

The influence of weather on fruit set

Weather Tape	Petal Fall Fruit Set Percentage (fruit/blossom * 100)	
	'Delicious'	'McIntosh'
Ideal flight weather	47.7	8.7
Good flight weather	22.5	3.1
Warm rain	20.9	4.1
Flight on day - 2	0.19	0.02
Flight on day - 3	2.7	0.5
Flight on day - 4	9.3	1.7
Flight on day - 5	15.0	3.1
Flight on day - 6	15.1	3.8
Flight on day - 7	5.4	2.0

*Constant parameters in the simulations

Colony Density: 2.5 colonies/hectare

Tree size: Semi-Dwarf

Orchard Design: xxxooo
x = 'Delicious'   o = 'McIntosh'

Table 5

The influence of orchard design and colony number on fruit set. *

Orchard Design	colonies/hectare	Petal Fall Fruit Set 'Delicious'	 'McIntosh'
oooxxx	2.5	22.5	3.1
	10.0	25.0	8.3
	20.0	25.0	10.5
	30.0	25.0	10.9
xxo	2.5	20.5	8.1
	10.0	24.3	18.1
	20.0	24.4	19.9
	30.0	24.4	20.0
xxxo	2.5	18.7	14.1
	10.0	22.8	26.6
	20.0	22.9	27.7
	30.0	22.9	27.8
xxxxo	2.5	17.4	26.3
	10.0	21.3	33.5
	20.0	21.5	34.2
	30.0	21.5	34.2
xxxxxo	2.5	16.3	26.3
	10.0	20.1	39.4
	20.0	20.2	39.6
	30.0	20.2	39.7
xxxxxxo	2.5	15.4	31.9
	10.0	19.0	44.0
	20.0	19.0	44.1
	30.0	19.0	44.2

* Constant parameters in the simulations

Weather Tape Used: Good flight weather

Tree size: Semi-Dwarf

x = 'Delicious' o = 'McIntosh'

'Delicious' percentages were achieved when trees were planted in a one 'Delicious' to one 'McIntosh' ratio.

In 'McIntosh' trees, the fruit set goal (10%) was not met in orchards with a one 'Delicious' to one 'McIntosh' tree ratio unless colonies were introduced at a rate of 20/hectare (Table 5). In an orchard with a two 'Delicious' to one pollinizer ratio, more than 2.5 colonies/hectare were needed to achieve the fruit set goal. In all other orchard designs where 'McIntosh' trees were outnumbered by more than a three-to-one ratio with 'Delicious,' the fruit set goal was met prior to petal fall with colonies introduced at a rate of 2.5/hectare.

As in the case of 'Delicious,' the greatest 'McIntosh' fruit set gains were achieved with additional colonies in the interval of 2.5-10/hectare. In McIntosh, the fruit set percentage increased as the ratio of 'Delicious' to 'McIntosh' increased. The opposite effect occurred on the 'Delicious' trees (i.e., as the 'Delicious'/'McIntosh' ratio increased, 'Delicious' fruit set decreased).

The Influence of Flower Viability and Colony Number on Fruit Set

Simulations were conducted to test if fruit set goals could be met in 'Delicious' and 'McIntosh' when flower viability was limited. The results of these simulations are summarized on Table 6. With flower viability as low as 40% (i.e., only 40% of the blossoms had the potential to set fruit), the 'Delicious' fruit set goal (10.8%) could be reached prior to petal fall with 2.5 colonies/hectare. The 'McIntosh' fruit set goal (10%) could be reached prior to petal fall with 2.5 colonies/hectare only if blossom viability was higher than 80%. 'McIntosh' required 10 colonies/hectare to reach its fruit set goal of 10% prior to petal fall when blossom viability was set at 40%.

When only 20% of the 'Delicious' blossoms had the potential to set fruit, 10 colonies/hectare were needed for the fruit set goal to be reached (prior to petal

Table 6

The influence of blossom viability and colony number on Fruit Set. *

'Delicious' and 'McIntosh' Blossom viability	Colonies/Hectare	Petal Fall Fruit Set	
		'Delicious'	'McIntosh'
100%	2.5	19.8%	15.6%
80%	2.5	18.4%	12.9%
60%	2.5	16.5%	10.0%
40%	2.5	13.5%	7.0%
	10.0	18.5%	14.0%
20%	2.5	8.6%	3.7%
	10.0	13.0%	7.9%
	20.0	13.4%	8.3%
	25.0	13.4%	8.3%
15%	2.5	6.7%	2.9%
	10.0	10.7%	6.2%
	20.0	11.15%	6.5%
	25.0	11.2%	6.5%

* Constant parameters in the simulations

Weather tape used = Good flight weather

Orchard Design = ooox

O = 'Delicious' x = 'McIntosh'

fall) (Table 6). Additional colony introduction up to 25/hectare could not prompt enough cross pollinations to permit the 'McIntosh' fruit set goal to be reached though. When blossom viability was set at 15%, 20 colonies/hectare were needed to reach the 'Delicious' fruit set goal prior to petal fall. With 'McIntosh' blossom viability set at 15%, again this variety's fruit set goal could not be reached regardless of the number of colonies introduced per hectare.

The Influence of Flower Quality and Weather on Fruit Set

In the version of REDAPOL used in these simulations, the quality of flowers, in terms of their probability of fruit set, could be initialized at the beginning of the run. An assumption used in the construction of the model was that blossoms lose their ability to set fruit as they age because of ovule degeneration. This assumption was based on the findings of Hartman and Howlett (1954) and their work with flower quality in 'Delicious.' Late developing blossoms were also predicted to have reduced probabilities of fruit set on their day of anthesis. For instance, blossoms opening on the first day of bloom ('King blossoms') were assumed to have a higher probability of fruit set (on their day of anthesis) than lateral blossoms opening later in the bloom period.

The influence of flower quality on fruit set was tested by simulating blooms that had decreasing versus constant flower quality. In the first group of simulations, 'Delicious' and 'McIntosh' blossoms had decreasing probabilities of fruit set with respect to their age (i.e., accumulated degree days since their day of anthesis) and period of opening during bloom. A second group of simulations was then conducted with blossoms having constant fruit set probabilities (0.999) regardless of their age or period of opening. Comparisons were then made between the resulting fruit sets under various weather conditions. In these simulations, all other orchard parameters: tree height, width, spacing, flowering spurs/meter of branch, and colonies/hectare were identical so that any differences in fruit set could be attributed to flower quality.

Under all weather conditions, final fruit set in both varieties was greater when flower quality remained constant during bloom (Table 7). Flower quality did not strongly influence the attainment of the 'Delicious' fruit set goal, however. Under conditions of constant flower quality, the goal was met on the same day as when flower quality was decreasing. The only exception was when 'ideal flight weather' conditions were simulated. In this case, the 'Delicious' fruit set goal occurred a day earlier under conditions of constant flower quality.

Conversely, 'McIntosh' fruit set was strongly influenced by flower quality, and final fruit set percentages increased greatly when flower quality remained constant (Table 7). Under all three sets of weather conditions, the 'McIntosh' fruit set goal could be met prior to petal fall if fruiting probabilities were constant. When ovule degeneration was simulated using decreasing fruit set probabilities though, 'McIntosh' fruit set was greatly reduced.

The Influence of Colony Density on Fruit Set Under Various Weather Conditions

Simulations were run to test if 'Delicious' and 'McIntosh' fruit set rates, under various weather conditions, could be increased by raising the number of honey bee colonies per hectare. The results of these simulations are summarized in Table 8 and Figures 1 and 2. In both 'McIntosh' and 'Delicious,' the fruit set rate was increased most by additional colonies when 'ideal flight weather' existed for the duration of bloom. The greatest increase in 'Delicious' fruit set occurred in the interval of 0.62-7.4 colonies/hectare. After this point, additional colonies did not significantly increase fruit set. At all colony/hectare densities and 'ideal

Table 7

The influence of blossom quality and weather conditions on fruit set. *

Weather	Petal fall fruit set constant fruiting probabilities 'Delicious'	Petal fall fruit set constant fruiting probabilities 'McIntosh'	Petal fall fruit set decreasing fruiting probabilities 'Delicious'	Petal fall fruit set decreasing fruiting probabilities 'McIntosh'
Ideal flight weather	65.4	19.6	51.6	6.4
Good flight weather	24.9	10.7	23.2	2.3
Warm flight weather	40.4	11.8	23.3	2.9

* Constant parameters in the simulations
Colony density: 2.5 colonies/hectare
Tree size: semi-dwarf
Orchard Design = xxxooo
x = 'Delicious'
0 = 'McIntosh'

Table 8

The influence of colony density on fruit set under various weather conditions. *

Weather	colonies/hectare	Petal Fall Fruit Set (Fruit/Blossom * 100) 'Delicious'	'McIntosh'
Good	0.62	14.95	0.94
	1.2	19.30	1.75
	2.5	22.49	3.14
	5.0	24.34	5.36
	7.4	24.87	7.00
	10.0	25.04	8.32
	12.3	25.00	9.27
Ideal	0.62	26.44	3.15
	1.2	37.43	5.38
	2.5	47.71	8.68
	5.0	55.23	12.88
	7.4	59.06	14.47
	10.0	61.55	15.16
	12.3	63.16	15.66
Warm rain	0.62	11.05	1.48
	1.2	16.64	2.56
	2.5	20.86	4.08
	5.0	26.06	5.33
	7.4	29.47	6.01
	10.0	30.46	6.32
	12.3	31.02	6.54

* Constant parameters in the simulations
Tree size: Semi-Dwarf
Orchard design = oooxxx
o = 'McIntosh' x = 'Delicious'

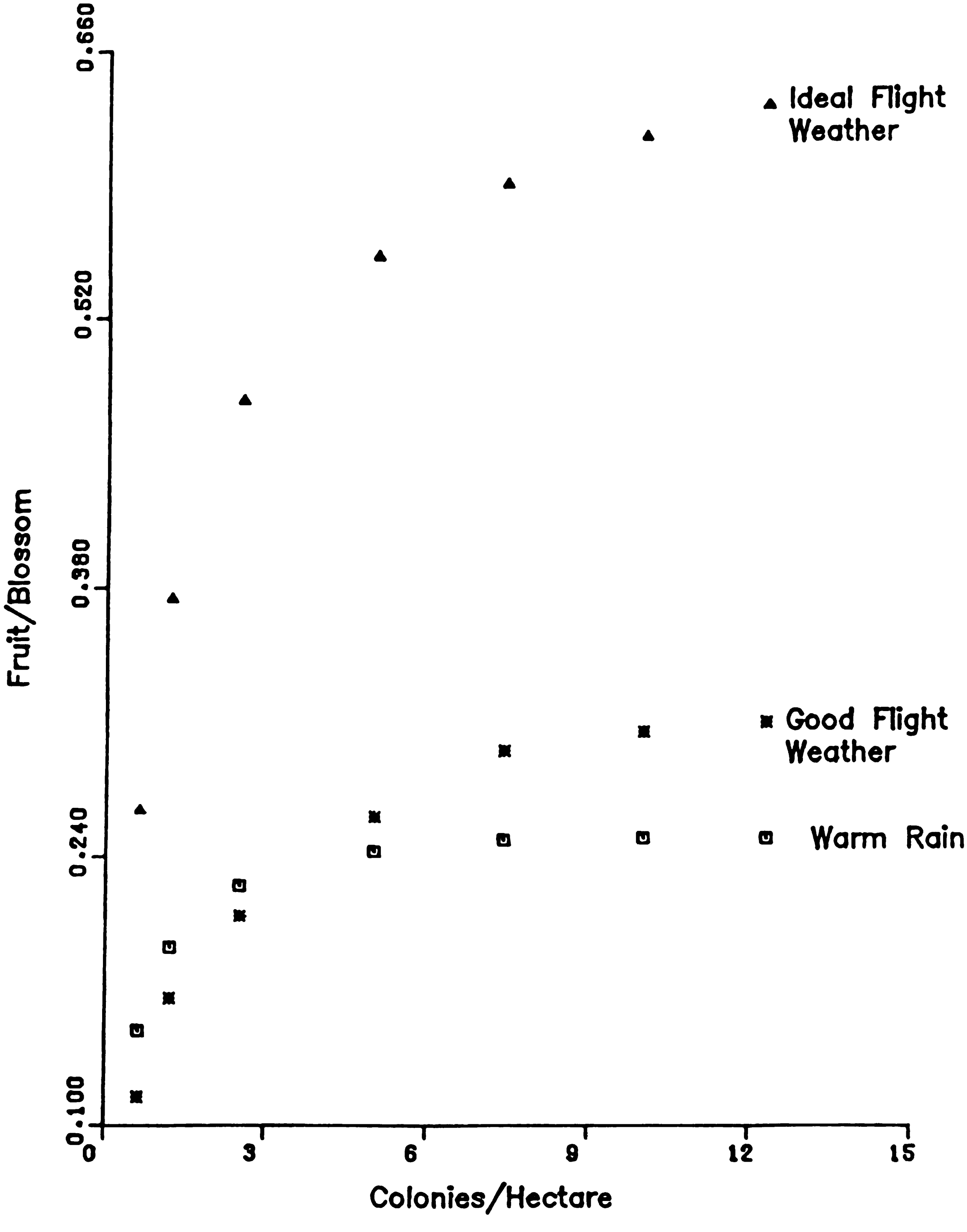

Figure 1. Predicted 'Delicious' Fruit Set Percentages Under Various Colony/Hectare and Simulated Weather Conditions.

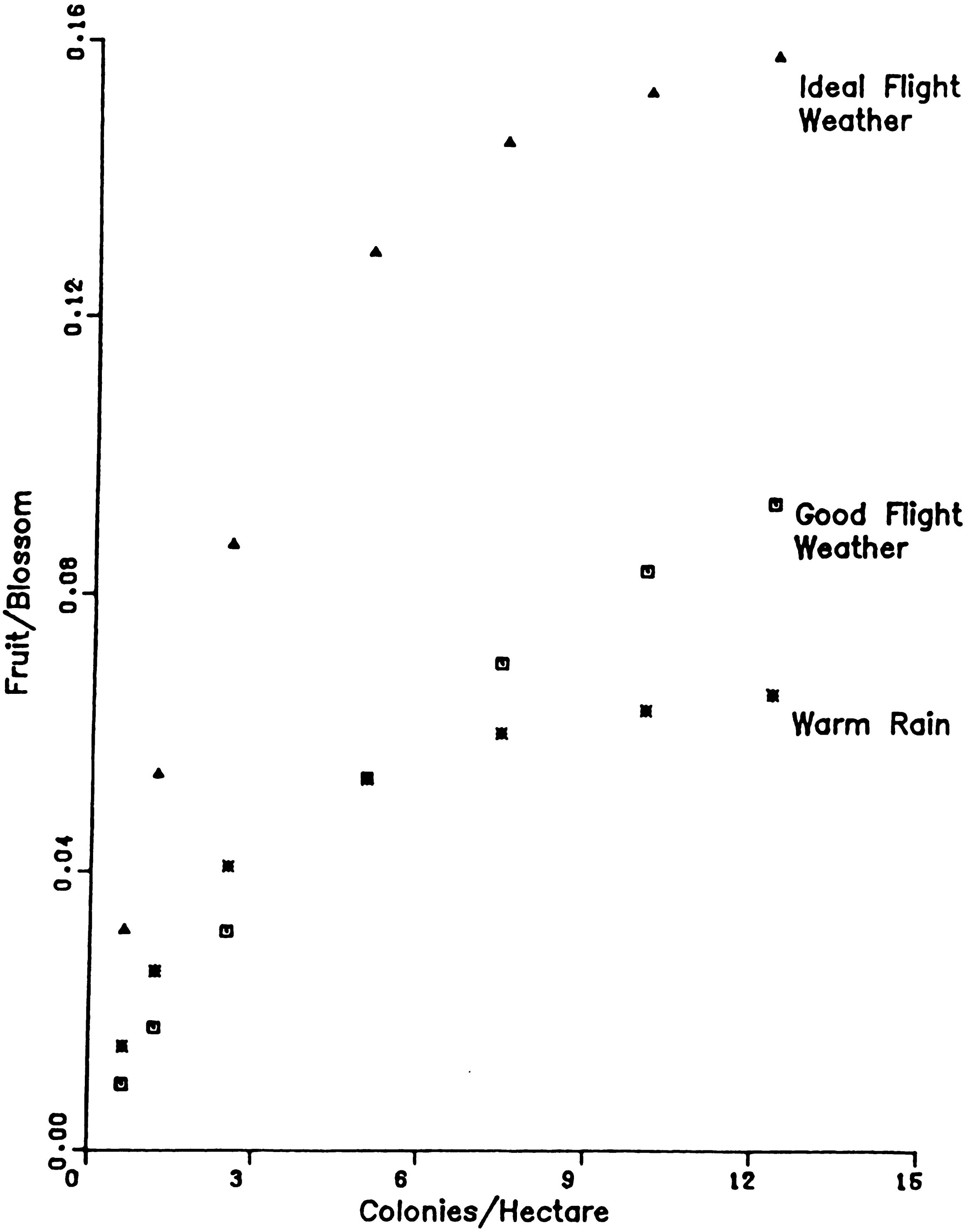

Figure 2. Predicted McIntosh Fruit Set Percentages Under Various Colony/Hectare and Simulated Weather Conditions.

flight weather' conditions, the fruit set goal for 'Delicious' was met on the third day of bloom (40.8 DD_5). Consequently, the increase in fruit set with additional colony introduction was essentially overset that would have required thinning to achieve good fruit size. Conversely, the 'McIntosh' fruit set goal (10.4% of the blossoms set fruit) was met under 'ideal flight weather' conditions at the end of bloom only when colonies were introduced at a rate of five or more per hectare (with the simulated orchard design) (Table 8).

Although fruit set in both varieties increased with additional colony introductions under both 'good flight weather' and 'warm rain' conditions (where flight weather was limited), the increase was not as great as under 'ideal flight weather' conditions. In both varieties, the fruit set rate did not increase greatly after more than 5 colonies/hectare were introduced. The fruit set goal in 'Delicious' was met on the eighth day of bloom under all colony/hectare densities and 'good flight weather' conditions, and on the third day of bloom (45 DD_5) under 'warm rain' weather conditions. Although 'McIntosh' fruit set increased with additional colony introduction, the fruit set goal (12% blossoms set fruit) was not met at any colony density under 'good flight weather' or 'warm rain' conditions.

DISCUSSION

According to our simulations, the factors most strongly affecting fruit set are the availability of compatible pollen, and the size of the foraging population on apples. Orchard design played an important role in attaining a desired fruit set goal, and 'Delicious' and 'McIntosh' trees planted in a one to one ratio resulted in the highest 'Delicious' fruit set values, even when planted in solid blocks. Conversely, fruit set values for 'McIntosh' were lowest when planted in a one-to-one ratio with 'Delicious.'

Predictions of low set on 'McIntosh' in one-to-one plantings can be attributed to the progression of flowering in the two varieties. 'McIntosh' blooms before 'Delicious' and has a lower degree day threshold for its progression of bloom. As a result, 'McIntosh' has more open blossoms during its pre-peak bloom interval than 'Delicious' and in the simulations would be the predominant apple pollen in the hive (during this interval). This would cause numerous cross pollinations on 'Delicious' blossoms opening early in bloom but would limit fruit set on 'McIntosh' (a self-incompatible variety) because of a dilution in compatible ('Delicious') pollen.

When simulations were run with higher 'Delicious' to 'McIntosh' ratios, 'McIntosh' fruit set increased to percentages more commonly encountered in the field. In commerical orchards, 'McIntosh' trees are often planted in arrangements with three or more times as many 'Delicious' trees so there is enough compatible pollen to often overset the 'McIntosh' trees. Hence, it has been concluded that 'McIntosh' does not have fruit set problems while in some situations 'Delicious' does. In the field, when 'Delicious' are planted at greater than three-to-one ratios with a pollinizer, 'Delicious' fruit set may in fact be poor in some years due to a dilution of pollinizer pollen in the hive.

The model also displayed a behavior often seen in the field where dwarf trees out produce semi-dwarf and standard plantings. Dwarf trees did not have as high a fruiting percentage as semi-dwarf or standard trees but did produce more bushels per hectare. The higher fruiting percentages predicted on the larger trees was probably a result of the distribution of cross pollinations. In standard or semi-dwarf orchards there were fewer trees per hectare and hence more cross-pollinations per tree. In the dwarf orchard there were more trees, each with comparatively fewer blossoms. Consequently, fewer cross pollinations took place per tree, but yields were higher because there were more blossoms per hectare.

Not surprisingly, weather was found to influence the rate of fruit set, especially if flight weather was restricted to a single day during bloom. The effects of weather on fruit set were exerted two ways. The first was progression of bloom which especially affected 'McIntosh' trees. Fruit set was higher in this variety under conditions of 'warm rain' than in 'good flight weather.' This was because higher temperatures programmed in the 'warm rain' tape progressed the blooms faster so that when flight weather did exist, there were more 'Delicious' blossoms open to serve as a compatible pollen source for the 'McIntosh'. The same effect was seen in both varieties when flight was restricted to one day during bloom. The conditions on the flight day were identical between weather tapes, but the maximum number of open 'Delicious' and 'McIntosh' blossoms occurred on day-6 of bloom (68-82 DD_5, 88-106 DD.). At this time a commercial sized apple crop was predicted to occur with a single day of 'ideal flight weather.'

Weather also affected fruit set because of its influence on honey bee flight. Weather tapes that restricted flight (i.e., 'good flight weather,' 'warm rain,' etc.) resulted in lower fruit set predictions compared to those based upon 'ideal flight weather' during bloom. When conditions for flight are limited, many blossoms do not receive cross pollinating visits for most if not all of their lives. This would explain the lower petal-fall fruit set percentages. Under 'ideal flight weather' conditions though, flight was not at all restricted, and the resulting fruit set was totally a function of orchard design and the influence of weather on the progression of bloom.

When honey bees were introduced at rates greater than 0.62 colonies/hectare, petal fall fruit set increased under all weather conditions. Adding more colonies was not necessary though, if fewer numbers allowed a fruit set goal to be achieved. This was because the time needed to reach the goal could not be significantly shortened by adding more colonies. In these simulations the additional fruit from introducing more colonies represented an overset that would have required thinning to achieve good fruit size.

It has been reported that compared to other varieties, 'Delicious' is less resistant to low temperatures just before and during bloom, and in some years and sites a high percentage of blossoms lose their ability to set fruit (Hartman and Howlett 1954). Although it has been suggested that this factor may be partially responsible for low yields in 'Delicious,' our simulations predicted that a full crop could be obtained with 2.5 colonies/hectare even if up to 60% of the blossoms were non-viable. If only 20% of the blossoms had a probability of setting fruit, a full crop could be achieved by introducing colonies at a rate of 10/hectare.

Although 'McIntosh' fruit set benefited more than 'Delicious' by additional colony introduction, it also required more colonies per hectare to reach its fruit set goal when blossom viability was low. Because 'McIntosh' bloom is chronologically shorter than 'Delicious' in the model (due to its lower degree day threshold temperature), the total time when cross-pollinations can occur in 'McIntosh' is more limited. When a high percentage of blossoms are non-viable, even more need to be cross pollinated (in both varieties) for a fruit set goal to be reached. Many 'McIntosh' blossoms were not cross pollinated at lower colony/hectare densities, and those blossoms that were, probably had lower fruit set probabilities (compared to 'Delicious') due to the rapid aging of 'McIntosh' bloom. Consequently more cross pollinations were needed for 'McIntosh' than 'Delicious' to set the same amount of fruit. This explains why 'McIntosh' fruit set increased more than 'Delicious' with additional colony introdctions, and required higher colony/hectare densities to reach a fruit set goal when blossom viability was low.

The fact that most 'McIntosh' blossoms were not cross pollinated early in bloom or on their day of anthesis was further evidenced by the results of simulations with constant and decreasing blossom quality (i.e., fruit set probabilities). When fruit set probabilities were held constant (at 0.999) for every blossom over it entire life, 'McIntosh' fruit set increased more than 'Delicious' regardless of the weather conditions. In the model, most cross pollination to 'Delicious' blossoms occur early in bloom and not long after their day of anthesis. This is when fruit set probabilities are relatively high,and consequently 'Delicious' fruit set was not increased as much by constant high fruit set probabilities as was 'McIntosh.'

During the development and validation of REDAPOL, the source of honey bees carrying compatible pollen (pollinators) was assumed to be the pivotal point in predicting fruit set. Pollinators were reported to originate from competition for nectar which forced some bees to move from tree to tree to obtain a full nectar load (Butler 1944, McGregor 1976). When competition and tree to tree movement were simulated using REDAPOL, the contribution to fruit set from this pollinator source was predicted to be minimal (i.e., less than 1 % of total fruit set), even when pollinizer trees were interplanted in 'Delicious' rows.

By far the greatest contributions to fruit set in our simulations, were attributed to honey bees that had acquired compatible pollen in the hive. In the field, this source of pollinators explains how fruit is set on self-sterile trees planted in solid blocks or in rows a considerable distance from the pollinizer. Our simulations predict that the majority of fruit set in both solid blocks and those interplanted with pollinizers is by honey bees that have acquired compatible pollen in the hive.

Results from these simulations could have profound implications with regard to recommendations on orchard design. If indeed the majority of pollinators are originating from pollen transfer in the hive, the ratio of 'Delicious' to pollinizer trees may be more important than their actual arrangement in the orchard. Our simulations support this conclusion, and predict optimum commercial sets on 'Delicious' trees planted in solid blocks at a one to one ratio with a pollinizer variety that blooms 1-2 days earlier.

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DEFINING THE POLLINATING POPULATION IN AN APPLE ORCHARD USING SCANNING ELECTRON MICROSCOPY

INTRODUCTION

Although the behavior of honey bees (Apis mellifera L.) foraging apple has been the subject of considerable study (g. v. Free 1960, Free 1966, Free and Spencer-Booth 1964, Robinson 1979), the sequence of events leading to the formation of a cross-pollinating population (i.e., honey bees carrying pollen that could initiate fruit set) has never been documented. Because apple crops produced on self incompatible trees (i.e., varieties that require pollination by an unrelated variety to initiate fruit set) are often quite large, it is evident that this cross-pollinating population may be of considerable size. Most often though, honey bees remain on the same tree during a foraging trip, and will return to it throughout the day. In self-incompatible varieties, this behavior alone could not initiate fruit set because cross-pollinations would not occur. Because when honey bees leave a tree, the next one visited is often an adjacent one in the same row (Free 1966, Free and Spencer-Booth 1964), recommendations concerning tree arrangements in orchards with self-incompatible varieties have stressed interplanting pollinizer varieties in the main cultivar rows (Latimer 1931, Brittain 1933, Burrell and MacDaniels 1931, Free 1962). This practice increases the chances of bee movement between trees of unrelated varieties, and reportedly results in a significant increase in cross pollination.

If reported observations on honey bee movement truly reflect the behavior of the foraging population, the transfer of pollen between two trees of unrelated varieties should indeed be a rare event, especially in solid block plantings or in isolated self-incompatible trees. Keeping in mind that only a varying percentage of a hive's foraging force is working apple, and that population is further subdivided into those finding adequate rewards on a single tree and remaining there, and those moving between trees of the same variety, the population of bees moving in cross pollinating directions (pollinators) is probably quite small. Hence, fruit set should be limited on all self-incompatible varieties, and ought to decrease significantly with distance from the pollinizer. However, this has not been found to occur consistently, which suggests that the portion of the foraging population with cross pollinating potential may be resulting from another set of conditions other than tree to tree movement.

The possibility that pollen transfer in the hive from contact between nestmates could be contributing to pollinator population was first suggested by Karmo and Vickery (1954). One way to test this would be to examine pollen carried on the bodies of honey bees working apple blossoms. Because honey bees show foraging fidelity to a single plant species, if pollen was not transferred in the hive, foragers ought to be carrying primarily one species of pollen on their bodies. To test this hypothesis, it would be necessary to accurately identify specific grains of pollen from different apple varieties and other plant species blooming in concert with apple, and then sample the pollens carried by honey bees foraging apple.

Scanning electron microscopy (SEM) can be used to identify pollen from different fruit varieties, because pollen grains have been found to differ in their exine patterns from variety to variety (Fogle 1977 a,b). Using SEM, pollen from different apple varieties and from non-apple species can be accurately identified on the bodies of foragers working apple blossoms, and on apple blossom stigmata. The purpose of this study was to define the pollinator population in an apple orchard using SEM, and determine if the transfer of compatible pollen is a constraint on fruit set in self-incompatible varieties.

MATERIALS AND METHODS

The Influence of Distance from the Pollinizer on Fruit Set

To test for the influence of distance from the pollinizer on fruit set, sites were selected in Leelanau County, Michigan based upon their arrangement of pollinizer and 'Delicious' trees. At Stanek and Sons' Orchard, three rows of 'Delicious' were followed by a row of 'McIntosh.' This pattern was continued for 14 rows. At Herman's Orchard three rows of 'McIntosh' were adjacent to five rows of 'Delicious' on their north side and four rows of 'Delicious' on their south.

During bloom at both sites, blossoms were counted on trees various distances from the pollinizer. One meter branch sections on four sides of the tree were chosen for these counts. After June drop (about three weeks after petal fall) the resulting fruit was counted. Seed from retained fruit on 'Delicious' trees various distances from the pollinizer rows was also counted at the Herman's Orchard.

Data from fruit set and seeds per fruit in rows various distances from the pollinizer were analyzed using an F-test. In cases where the F-test prompted a rejection of the null hypothesis, a Tukey's W multiple comparison test was performed (Tukey 1953).

Analysis of Pollens on Honey Bees and Apple Stigmata

Honey bees foraging 'Delicious' (Millerspur) and 'McIntosh' (Macspur) blossoms at the Michigan State University Horticulture Research Farm (in East Lansing, Michigan) were captured periodically during the day, placed in separate vials and immediately frozen. 'Delicious' and 'McIntosh' blossom stigmata were also sampled daily during bloom, stored separately in vials, and frozen until analyzed. Pollen was then collected from 'Delicious,' 'McIntosh,' and other fruit trees and plants blooming in concert with apple to aid in the identification of pollens on honey bees and blossom stigmata.

Millerspur 'Delicious' trees at the M.S.U. Horticulture Farm were planted in solid rows (5-6 trees per row) and were approximately the size of standard trees (i.e., more than 8 m high and 6 m wide). On one side of the Millerspur 'Delicious' was a row of Red Prince 'Delicious' (4 m away) and on the other, a row of 'Spartan' trees (9 m away). The 'McIntosh' used in this study were planted in a three row 32 tree solid block. These trees were also more than 8 m tall and were spaced so closely the planting ressembled a hedge row The trees were bordered on the east by flowering tart cherry, on the north by a road, on the south by a meadow, and on the west by a young tart cherry planting that was not yet flowering.

Pollen from the bodies of honey bees captured while working 'Delicious' and 'McIntosh' trees was sampled by rolling the insect's body over on aluminum SEM stub coated with adhesive. The sample was sputter-coated with gold for three minutes. Non-germinated pollen grains were then identified as self-, cross-, or non-apple pollen by comparing their exine paterns with pollen samples collected from fruit trees and other plants.

Frozen floral stigmata were prepared for SEM examination by placing them on an aluminum stub pretreated with adhesive. The stigmata were then sputter coated with gold for three minutes and examined for the presence of self-, cross- and non-apple pollens. All samples were analyzed with a JEOL JSM-35 scanning electron microscope operated at 15kV.

RESULTS

Effect of Distance from the Pollinizer on Fruit Set

At both orchard sites, fruit set did not differ significantly between 'Delicious' rows with respect to their distance from the pollinizer (Table 1). At the Stanek and Sons' orchard 19.8% of the 'Delicious' blooms set fruit in rows next to the pollinizer, while 16.5% set fruit on trees one row away. At Herman's orchard percentages of blossoms setting fruit ranged between 14.8% (trees three rows away from the pollinizer) and 17% (trees two rows away from the pollinizer). Trees four rows away from the pollinizer had statistically equivalent fruit set(16.7%) to those adjacent to the pollinizer row (Table 1.).

Seeds per fruit (from 'Delicious' trees) was greatest on trees next to the pollinizer (on the east side), although seed number did not decrease accordingly with increasing distance from the pollinizer row (Table 2). Seeds per fruit ranged between 3.70 (trees three rows away from the east side of the pollinizer) and 6.89 (trees next to the pollinizer on the east side). Seeds per fruit on trees four rows away from the pollinizer was not significantly different than in rows next to the pollinizer (on the west side).

SEM Analysis of Pollens on Honey Bees and Blossom Stigmata

Pollen grains from different apple varieties and competitive plants could be identified by size, shape, and exine patterns. Millerspur 'Delicious' pollen grains were oblong, porous, and had a characteristic exine pattern (Figure 1A). 'McIntosh' (Macspur) pollen had the shallowest exine pattern of any apple variety examined, and could be separated easily from several other varieties ('Delicious', 'Gallia Beauty', 'Rhode Island Greening') (Figure 1). Although pear, tart cherry, and plum were also similar in shape to some apple varieties (and to each other)

Table 1
The influence of distance from the pollinizer row on 'Delicious' fruit set in two Michigan orchards.

Site	Rows away from pollinizer	Sample Size	Proportion of blossom setting fruit (Mean ± S. D.)
Stanek and Son's Orchard	1	10	.165 ± .043 a
	Next to	15	.198 ± .03 a
Herman's Orchard	Next to	16	.164 ± .030 a
	1	16	.150 ± .030 a
	2	16	.170 ± .028 a
	3	16	.148 ± .025 a
	4	8	.167 ± .041 a

Means followed by the same letter are not significantly different at the .05-level as determined by the F-test.

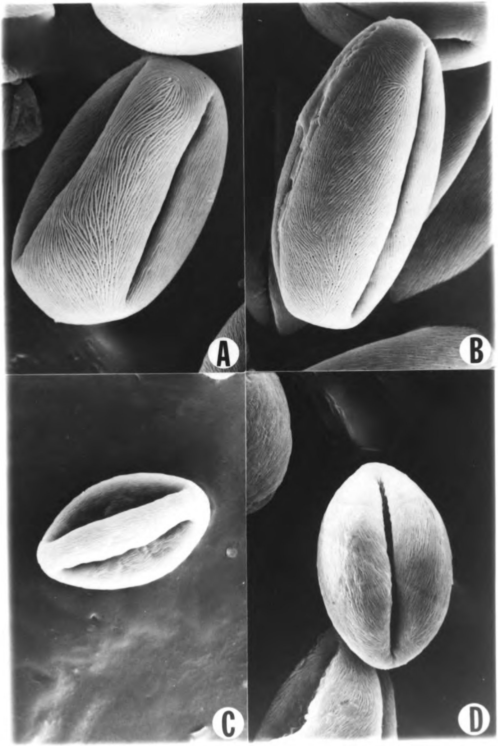
TABLE 2

Number of seeds per fruit on 'Delicious' trees various distances from the pollinizer.

Rows from Pollinizer	Direction	N	Mean number of seeds per fruit ± SD.
4 Away	E	20	4.75 ± 1.77 a
3 Away	E	20	3.70 ± 1.89 a
3 Away	W	20	3.90 ± 1.86 a
2 Away	E	20	3.80 ± 2.12 a
2 Away	W	20	4.05 ± 1.73 a
1 Away	E	19	4.53 ± 2.20 a
1 Away	W	20	4.90 ± 2.17 a
Next to	E	19	6.89 ± 3.20 b
Next to	W	20	5.30 ± 2.62 a

Means followed by the same letter are not significantly different at the 5% level as determined by Tukey's W method.

Figure 1. Scanning electron micrographs of apple pollen grains.
A = Millerspur 'Delicious', B = Macspur 'McIntosh'
C = 'Gallia Beauty', D = 'Rhode Island Greening'.
All magnifications are 1800x


A
B
C
D

their exine patterns permitted them to be easily distinguished (Figure 2). Dandelion and yellow rocket were also readily discerned by their characteristic shape and exine patterns (Figure 2).

When pollen was removed from honey bees working 'Delicious' (Millerspur) and 'McIntosh' trees, and non-germinated pollen grains were identified, every apple forager examined was carrying at least some cross pollen, although in a few cases (mostly in the afternoon hours) no detectable self-pollen. Non-apple pollen was also found on a majority of honey bees (Table 3 and Figure 3).

Compatible pollen was found to comprise at least half of the pollen types carried by foragers working either apple variety (Table 4). Non-apple pollens comprised 30.2% of the types carried by 'Delicious' foragers, and 23.2% of those working 'McIntosh.' These percentages varied widely though, during the day. Self-pollen made up 15.0% and 20.6% of the types carried on 'Delicious' and 'McIntosh' foragers respectively, but these percentages also had a large variance.

When apple blossom stigmata were examined for the presence of compatible pollen, grains could easily be identified and classified as cross-, self-, or non-apple pollen (Figure 4). In both varieties, when pollen was found on the stigma, a portion of it was always from an unrelated variety. Of all the 'Delicious' stigmata examined, 76.9% contained some cross-pollen (Table 5). When 'McIntosh' stigmata from a three row 32 tree solid block arrangement were examined, 91.3% were found to have cross-pollen. Self-pollen was also found on a majority of 'Delicious' and 'McIntosh' stigmata (73.1% and 82.6% respectively), and non-apple pollen was found in some instances (Table 5).

Figure 2. Scanning electron micrographs of pollen from species blooming in concert with apple. A = Tart Cherry (720x), B = Stanely Plum (720x), C = Bartlett Pear (1800x), D = Bosc Pear (660x), E = Dandelion (*Taraxacum* spp.) (440x), F = Yellow rocket (Barbarea spp.) (1300x).

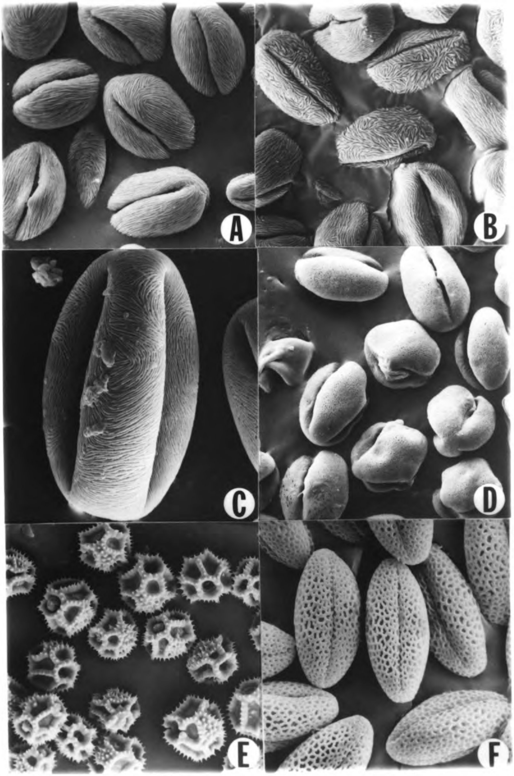

A
B
C
D
E
F

Table 3

Percentages of honey bees carrying cross-, self, and non-apple pollen while foraging 'Delicious' and 'McIntosh' trees.

Variety	Sample Size	% carrying compatible cross-pollen	% carrying self-pollen	% carrying non-apple pollen
'Delicious'	19	100%	84.2	89.5
'McIntosh'	15	100%	87.7	93.3
Total Honey Bees	34	100%	88.2	91.2

Figure 3. Scanning electron micrographs of pollens carried by honey bees foraging 'McIntosh' trees at the Michigan State University Horticulture Farm.

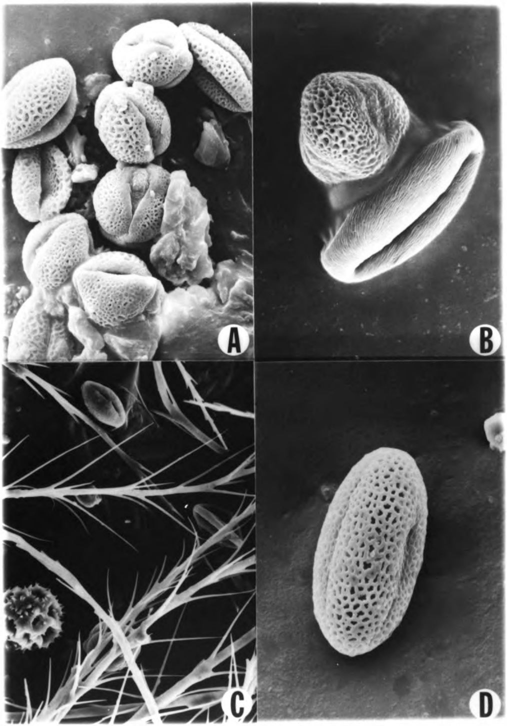

A
B
C
D

Table 4

Percentages of various pollen types carried by honey bees foraging apple.

Variety Being Foraged	Sample Size	% Self pollen	% Cross pollen	% Non-Apple pollen
'Delicious'	19	15.0 ± 7.6	51.6 ± 10.3	30.2 ± 11.4
'McIntosh'	15	20.6 ± 11.4	56.2 ± 13.3	23.2 ± 10.4

Figure 4. Scanning electron micrographs of pollinated apple blossom stigma: A and B are from 'McIntosh' blossoms, while C and D are from 'Delicious blossoms.

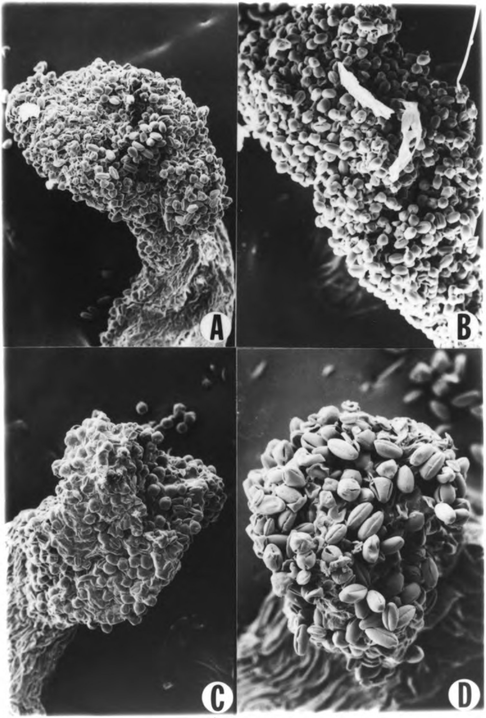


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TABLE 5

Percentages of apple blossom stigmata with self-, cross-, and non-apple pollens.

Variety	Sample Size	% with self-pollen	% with cross-pollen	% with non-apple pollen
'Delicious'	26	73.1	76.9	77.7
'McIntosh'	23	82.6	91.3	17.4

DISCUSSION

Although honey bees are responsible for the majority of fruit set in apple orchards especially those containing self-incompatible varieties (McGregor 1976), the size of the honey bee population capable of cross-pollinating blossoms (pollinators) has never been determined. From our analysis of pollen from apple foragers and blossom stigmata, it appears that this population may indeed be larger than previously suspected. Furthermore, in our study the size of the pollinator population on a tree did not seem to be strongly influenced by the tree's distance from the pollinizer.

It has been assumed that honeybees cross pollinate blossoms while moving from tree to tree in search of nectar. Several authors have shown decreases in fruit set with distance from the pollinizer, and have explained their results using this assumption (Williams 1959, Free 1962, Free and Spencer-Booth 1964). Although some fruit must surely be set this way, tree to tree movement does not explain how fruit is set in solid blocks of self-incompatible trees or in rows that are a considerable distance from the pollinizer. Furthermore, a decrease in fruit set has not been shown to consistantly occur, and often the differences in fruit set with increased distance from the pollinizer are not great (Free and Spencer-Booth 1964). These results in conjunction with our data suggest that cross-pollinating honey bees must be originating from a source other than movement from tree to tree.

Karmo and Vickery's (1954) suggestion that pollen may be acquired by foragers in the hive from contact among nestmates could help explain the wide range of pollens found on apple foragers in this and other studies (Kendall and Solomon 1970, Free and Williams 1972). In our investigation, the use of SEM to accurately identify apple pollens to variety provided a new perspective on the pollen types carried by honey bees, and their approximate distance from the tree being foraged. In many instances, varieties of pollen on honey bees were from trees more than 30 m away from where the bee was captured. It is doubtful that honey bees would have foraging areas that included several apple varieties and unrelated plant species, because these insects have been reported to remain primarily on the same tree when working apple and at best visit two trees during a foraging trip (Free and Spencer-Booth 1964, Free 1966).

If honey bees carried pollen only from species they were foraging, the apple foragers in our samples should have had only two species or varieties of pollen on their bodies. These bees would also be relatively rare since a majority of bees find adequate reward on a single variety and do not move from it. In our study, every apple forager examined had some pollen from an unrelated apple variety on her body. Although in a few cases we could not detect self-pollen, it should be noted that only non-germinated grains were counted in these samples, so self-pollen may have existed but in a germinated state.

Our results showing pollen from various plant species on apple foragers is in agreement with earlier work by other authors (Kendall and Solomon 1970, Free and Williams 1972). In previous studies, however, pollens (other than non-apple types) were classified as "fruit pollen" (Kendall and Solomon 1970) or "predominant species" pollen (Free and Williams 1972) without regard to specific varieties. Consequently, it was assumed that these pollens were from the main species being foraged when in fact, they may have been from several different varieties or even non-apple species.

The pollen grains found on honey bees are apparently located in areas where contact with a blossom's reproductive structure is possible. In our samples, there appeared was no shortage of compatible pollens on either 'Delicious' or 'McIntosh' stigmata. Even though some pollens directly on the stigmatic surface were not visible, nor were pollen tubes or signs of fertilization, in conjunction with our data on fruit set with distance from the pollinizer, it appeared that some compatible pollen was fertilizing ovules regardless of the tree's distance from the pollinizer.

Because tree to tree movement does not seem to be increasing fruit set in all instances, interplanting pollinizer trees within blocks of the main variety may not be necessary. What may be more important is the ratio of pollinizer to main variety trees, and the timing of their blooms (DeGrandi-Hoffman 1983). Ideal pollinizers would be those that bloom heavily before the main variety. This would cause honey bees to establish foraging areas on the pollinizer first, so that when the main variety bloomed, the existance of compatible pollen in the hive would be assured. This could permit honey bees working the main variety to acquire sufficient compatible pollen in the hive, and allow them to leave in a potential cross pollinating state.

The use of SEM has given us the ability to identify pollen to species and variety, and has lead us to conclude that a majority of honey bees working apple are carrying compatible pollen. Furthermore, the distribution of cross-pollinating honey bees is apparently not related to the trees' distance from the pollen source. Even in solid block plantings ('McIntosh' trees at the MSU Horticulture Farm) honey bees were found carrying pollen from several other apple varieties and species of plants. These results cannot be explained by tree to tree movement of honey bees, which has lead us to conclude, as Karno and Vickery (1954) did, that honey bees may be transferring pollen in the hive during contact with nestmates.

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GENERAL THESIS SUMMARY

One of the stronger arguments supporting a systems approach to problem solving is that during the phases of system description and validation, insights and new perspectives on the relationships between the system's components are inevitably gained. This argument has held true in the development of REDAPOL, because during this model's construction and validation, explanation on the source of honey bees with cross-pollinating potential (pollinators) and the reasons why 'Delicious' trees may under set in some years and sites have been obtained. As a consequence, recommendations on 'Delicious' and pollinizer tree arrangements to maximize fruit set have been derived, and colony/hectare requirements and the timing of colony introduction that are specific to the orchard and weather in a given year have also been developed.

The key to the model's ability to predict fruit set rates has to center around predictions on the size of the pollinator population. Field studies and simulations have indicated that the size of this population is far too large to be explained by tree to tree movement alone, and that transfer of pollen among bees in the hive may indeed be the primary source of pollinators. This finding has created revised recommendations on choices of pollinizer varieties, and their arrangement with 'Delicious' trees in orchards.

A large part of the problem with 'Delicious' fruit set may be the choice of pollinizer variety and orchard design. When pollinizer trees bloom after 'Delicious', the predominate apple variety in the hive during the first days of 'Delicious' bloom has to be 'Delicious' pollen. This type of pollen will not set fruit on 'Delicious' trees, and explains why king blossoms rarely set when 'Golden Delicious' (which blooms after 'Delicious') is used as a pollinizer in Michigan orchards. If a pollinizer variety is chosen that blooms before 'Delicious', the next constraint on fruit set may be the ratio of 'Delicious' to pollinizer trees in the orchard. Simulations have shown that when one variety of tree greatly outnumbers another (as often seen in 'Delicious' orchards), compatible pollen is diluted in the hive and can limit fruit set. In 'Delicious' orchards the highest fruit set percentages were obtained with simulations of one to one ratios of 'Delicious' and pollinizer trees planted in solid blocks.

During the development of REDAPOL the need to express the progression of bloom in physiological time units (accumulated degree days) became apparent, because of the variation in bloom length from year to year. Using the accumulated degree days required for peak bloom in each variety as a fixed point, threshold temperatures for 'McIntosh' (Macspur sport) and 'Delicious' (Millerspur and Red Chief sports) were defined by minimizing the variance between sites in the degree days needed to reach peak bloom. Although this method needs further testing, it may be a means to describe threshold temperatures for the progression of bloom in other apple varieties.

It has been concluded that although all apple varieties are related in some way, their threshold temperatures for the progression of bloom probably differ. For example, the threshold temperature for 'Delicious' bloom was determined to be $5^{o}C$ while for 'McIntosh' it was $1^{o}C$. This finding has interesting repercussions with respect to the aging of bloom and the availability of compatible pollen. In years when temperatures during bloom are low ($2\text{-}4^{o}C$), 'McIntosh' bloom will continue to progress while 'Delicious' bloom will not. As a consequence, when temperatures rise and conditions become suitable for honey bee flight, the availability of 'McIntosh' pollen may be a severe constraint on

'Delicious' fruit set. When weather tapes containing cooler temperatures were used in simulations, REDAPOL demonstrated this behavior.

Because modeling pollination and fruit set systems permits crop size to be predicted and managed, crops that rely on honey bees for cross-pollination and seed set have a distinct advantage over other crops with regards to consistancy and control of production. By establishing desired blossom to fruiting percentages (fruit set goals), honey bee colonies can be introduced and removed strategically so that crop size can be controlled. Further developments on honey bee repellent sprays could be the next step in enhancing fruit set control, because with them the effectiveness of colony removal to halt fruit set could be increased, especially in orchards with relatively large indigenous bee populations.

It is often said that models are never really completed because they can always be refined and elaborated upon. Future elaboration of REDAPOL will be directed at further validation and means for grower implementation. Before the model can be used by growers, sampling schemes will have to be developed so that orchard parameters can be entered into the model consistantly. In some orchards honey bee colonies are not introduced because feral bee populations (or those from a neighbor's hive) are large enough to produce commercial sets. REDAPOL could still be used in these orchards, by developing a plan to sample trees for honey bees early in bloom (while monitoring weather conditions), and then estimate indigenous colony/hectare densities by using the functions in the model that predict honey bees/tree in reverse order.

Pollination and fruit set modeling could represent the future of applied pollination research, because it can add a new consistancy in the production of honey bee pollinated crops. Similar models could be constructed for cotton, sunflowers, soybeans, and any other crops requiring cross pollination by honey bees. No longer will colony/hectare recommendations and timing of colony introduction and removal for various crops be the product of guesswork and previous practices. Instead, pollination and fruit set modeling will produce recommendations that are specific for the year and site in question, and permit pollination to be a compatible part of integrated crop management programs.