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FACTORS AFFECTING THE FLIGHT RESPONSES OF SELECTED PEST APHIDS
(HOMOPTERA: APHIDIDAE)

by

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Introduction

Insect migration and the migratory behavior of insects has long been a subject of interest to the entomologist.

The earliest account of insect migration occurs in the Bible. Here many accounts of insect movement are noted. The early reports of insect migration are concerned primarily with mass movements of insects, generally and most noticeably moving in the same direction (C. G. Johnson, 1963).

The definitions of migration are as numerous as they are varied. Rainey (1960) states that migration is simply "a seasonal displacement of populations." Kennedy (1961) defines migration as a "persistent, straightened-out movement with some internal inhibition of the responses that will eventually arrest it." Williams (1958) believes that "migration is a continued movement in a more or less definite direction in which both movement and direction are under the control of the animal concerned." Schneider (1962) proposed that migration is a "prolonged escape movement with a tendency to maintain the direction and to abandon definitely or periodically a habitat."

Most entomologists, until recently, thought of dispersal and migration as separate functions. Schneider (1962) defined dispersal as the "lengthening of the mean distance between neighboring individuals." Dispersal was believed to be a passive movement. Locusts, which have directional control of their flight, are displaced along wind trajectories (C. G. Johnson, 1961). This evidence removed the distinction between dispersal and migration.

There are a great many insect migrants which appear to be adapted to migrate and disperse at the same time (C. G. Johnson, 1961). The aphids are a typical example of this "dispersive migration."

The cause of aphid migration appears to be two-fold. To complete their annual life cycles, many aphids change host plants at various times of the year. The flight resulting from an alternation of hosts may be termed migration. The second and perhaps the more common explanation of aphid migration is overcrowding and the changes in host plant tissue produced by the feeding aphid, and climatic factors, which cause an increase in the production of alate aphids. When alate aphids become flight mature, they will take off under suitable conditions and migrate to a more suitable host.

Aphids are light in weight and have relatively large wings that enable them to be carried by the wind. If wind currents and climatic conditions are suitable, an alate aphid has the potential ability to migrate great distances. This ability was observed by Elton (1925) when he recorded Cinara piceae (Panzer), a spruce aphid, on snowfields at Spitzbergen. The nearest spruce host was more than 800 miles away. This striking observation has opened the door to much speculation about the flight ability and flight behavior of alate aphids.

Many aphids are serious pests of plants because of their feeding habits and their ability to transmit virus diseases. Outbreaks of aphids caused by a migratory flight may cause great damage and loss to crops that were previously uninfested.

Before any type of migratory control can be developed, a knowledge of the factors affecting flight ability and flight behavior must be known.

Such factors as temperature, light, wind, relative humidity and age of the aphid have been studied to some extent by previous investigators. These investigations have been mainly concerned with aphids not common to the central United States.

It is the purpose of the present study to attempt to determine some of the critical factors that influence some flight responses of certain pest aphids common to the central United States.

Review of Literature

Atmospheric displacement of insects is a well-known phenomenon. Much work has been done at Rothamsted, England, on the migration and dispersal of insects. Glick (1939) has done substantial work in tracing insect movement in the south central United States by means of airplane trapping.

The displacement of insects in the air is almost entirely dependent on the atmospheric conditions (Wellington, 1945). Wellington made several studies trying to determine the various atmospheric factors that are important in the vertical and horizontal distribution of insects. Wellington put special emphasis on the effect of temperature and pressure on insect activity. He found that pressure at an equivalent height of 12.5 kilometers caused inactivity of the insects and that insensibility came at 13.6 kilometers.

Glick (1939) reported insect and spider catches at 20 to 15,000 feet. He found some Hymenoptera and Homoptera at 14,000 feet. The lack of insect density at high altitudes, i.e., 13.6 kilometers, tends to minimize the importance of the effect of atmospheric pressures that was reported by Wellington (1945).

In further experimentation, Wellington found that the minimum temperature for activity in the Homoptera was around 12.7° C. He noted that any insect cooled below its minimum flight temperature invariably folded its wings in the normal rest position. This fact is important when considering the factors affecting fallout of insect migrants. His experiments clearly showed that temperature was the limiting factor in determining whether an insect could survive high altitude displacement. If active flight is the only means by which an insect can maintain altitude, it will surely follow the laws of gravity and fall out when it reaches its minimum flight temperature. The only remaining explanation of insect displacement is that the insect is supported by vertical atmospheric currents (Wellington, 1945).

Wind has both a horizontal and vertical component. The vertical component consists of mechanical turbulence and thermal convection (Wellington, 1945).

Mechanical turbulence arises from frictional sources and is usually confined to a layer below 3,000 feet. Thermal convection results from the heating of land surfaces. The warm ground radiates heat into the air that may form air pockets and rise. As these thermal pockets rise they may unite with other thermal pockets and form what is commonly known as a thermal. On a normal day, thermal convection usually takes place below 10,000 feet, but in unstable air conditions (i.e., thunderstorms) thermal convection may result as high as 50,000 to 60,000 feet (Jensen, 1963).

Because of the scattered nature of thermals, the presence of downdrafts, and the short life span of a thermal, its use as a long range

dispersal medium leaves serious doubts. It does possess the ability to distribute insects over a relatively short distance (Wellington, 1945). Mechanical turbulence has a distinctly fluctuating nature because of the earth's irregular surface. The consequent fluctuating air currents would be quite unsuitable for long range displacement. The proper combination of convection and turbulence appears to be necessary for any long range displacement by either of these means (Jensen, 1963).

A better explanation of long range displacement of insects seems to be displacement by low level jet stream. The low level jet stream is found over continental land surfaces subjected to strong periodic heating and cooling. If the vertical velocity of the jet stream is adequate, long range dispersal of insects could occur by this phenomenon (Wellington, 1945).

The aphids used in the present study are pest aphids common to the central United States, with the exception of Aphis fabae (Scop.).

The majority of the present work was done with the black bean aphid (Aphis fabae) and the greenbug (Schizaphis graminum). The black bean aphid is a known migrant and the majority of the work on aphid migration has been done with this aphid (C. G. Johnson, Taylor and Haine, 1957).

Schizaphis graminum (Rondani) is probably the most destructive aphid attacking small grains in this country (Peairs and Davidson, 1961). It is strongly suspected to be a long range migrant, moving from the southern United States to the North (Hodson and Cook, 1960). The ecological effects of temperature, humidity, and light on the greenbug have been studied to some extent by previous investigators (Wadley, 1931; Daniels, 1963).

Other aphid species were used in the present study, but were of secondary importance. The apple grain aphid, Rhopalosiphum fitchii

(Sanderson) attacks apples in areas of the Midwest. This aphid usually remains on the apple only a short time, then migrates to grains or grasses. The English grain aphid, Macrosiphum avenae (Kirby), is common to the grain growing areas of the Midwest. It is an economic pest of corn, oats, rye, wheat, timothy and other grasses. The corn leaf aphid, Rhopalosiphum maidis (Fitch), is a common pest of corn and sorghums. It is suspected that long range migration may occur at the time of tasseling (Peairs and Davidson, 1961). The pea aphid, Acyrtosiphon pisum (Harris), is a serious pest of forage crops, especially alfalfa. The migratory status of this aphid is uncertain, but short migratory flights are known to occur (Anonymous, 1964).

Aphid migration, like other insect migration, is caused by a combination of neurophysiological and ecological factors. The neurophysiological factors cause the persistent flight, while the ecological factors determine when flight occurs (C. G. Johnson, 1963).

Aphids give birth parthenogenically to nymphs. These nymphs will develop into either apterous or alate adults. The alate nymphs have wing pads and after the final moult, the wings are fully formed. Taylor (1957) defined the teneral period as "the interval between eclosion of the alate imago and flight, when flight is not extrinsically activated or inhibited." The behavior of aphids during the teneral period is very consistent. After moulting, they walk freely about until they find a suitably sheltered place and then settle down. Once they have settled down, the wings rapidly expand and the stylets are inserted in the host plant. After sitting motionless for a period of time, the insects suddenly withdraw their stylets and walk

up the leaf on which they have been sitting. They then walk about until they find a suitable take-off point and fly within a few seconds (Taylor, 1957).

Under favorable conditions of temperature, light, and wind, the alate aphid will move to the top of the plant and take off. If the aphid is hindered by excessive winds, she will attempt several times to take off and will eventually take off in winds stronger than those normally rejected (Haine, 1955).

In Aphis fabae, the length of the teneral period between moulting and flight depends on temperature. An increase in temperature causes the teneral period to shorten and is later followed by an increase in the rate of take off (C. G. Johnson, and Taylor, 1957).

If the aphid reaches flight maturity during the night or in an environmental temperature below its flight threshold, she will remain on the plant without reproducing and with her stylets inserted. She will remain like this until daylight when the temperature threshold for takeoff is reached (Cockbain, 1961d; C. G. Johnson and Taylor, 1957; Taylor, 1957).

In field experiments, utilizing a Johnson-Taylor segregating trap, Taylor (1957) determined the take-off thresholds for A. fabae. He found that the results obtained from these trap catches are accurate and comparable to laboratory experiments (C. G. Johnson and Taylor, 1957). The temperature threshold for wing beating and flight of Aphis fabae was investigated by Cockbain (1961d). He found the median temperature for wing beating, horizontal and upward flight to be 6.5°C, 13.0°C, and 15.0°C, respectively.

There are three common techniques for studying aphid flight behavior, each technique being capable of investigating a particular phase of flight behavior.

The most natural approach involves the use of a free flight chamber in which an aphid is allowed to fly freely. This technique gives the investigator an opportunity to observe the willingness of an aphid to fly with a minimum of extrinsic hindrance or stimulation (Kennedy and Booth, 1963; Chiang, 1963; Legge, 1962).

The simplest and most direct approach to aphid flight behavior is that of simply dropping an aphid and seeing if flight occurs. This is a means of measuring an aphid's ability to fly upon an initial stimulation. This technique is a logical starting point for aphid flight studies.

The final approach to the study of aphid flight behavior is flying an aphid tethered to a pin. This technique gives the investigator an opportunity to fly an aphid to exhaustion by continually stimulating it to fly (B. Johnson, 1958; Cockbain, 1961c).

Aphids, unlike most insects, fly with their body axes almost vertical and the plane of wing vibration nearly horizontal. After take-off the aphid exhibits a strong vertical flight, but it also at times hovers with some horizontal movement (B. Johnson, 1956).

Aphids alighting on plants after flight wander, probe, and sometimes settle if the plant is suitable and if flight has been extensive enough (B. Johnson, 1958; Kennedy, 1958). The longer the aphid flies the stronger will be the settling response. If the response is strong enough, settling is followed by probing, feeding, nymph production, resumption of embryogenesis and wing autolysis (B. Johnson, 1958; Kennedy, 1958).

Many aphid species fly only for a few days after completing teneral development. During this time, growth of embryos is halted until the flight muscles autolyze (B. Johnson, 1953). Within a few days after settling on a host plant, alate aphids undergo a physiological change. This change is seen in the breakdown or autolysis of flight muscles and the resumption of embryo development. Muscle autolysis and the subsequent reproduction can be delayed by preventing the alate aphid from settling. This can be accomplished by denying the aphid a host or substituting an unsuitable host (B. Johnson, 1957).

Some tree aphids are exceptional, maintaining their ability to fly and reproduce throughout life. Haine (1955) showed this to be true in some species of the tribe Calliperini.

The final loss of flight ability appears to result from the autolysis of flight muscles; there is also a concurrent reduction in the activity of the aphid (B. Johnson, 1957).

In laboratory tests employing free flight, Legge (1962) found that Myzus persicae took off and flew up to 85 minutes. Most first flights lasted between 40 and 70 minutes.

Kennedy and Booth (1963) in experiments with a free flight chamber noted a long initial flight that may last up to an hour. The aphid will alight but is still capable of a number of similar flights, each of decreasing duration.

Laboratory tests show that flights to apparent exhaustion of Aphis fabae do not affect its fecundity and longevity (Cockbain, 1961c). This indicates that long migratory flights will not affect the aphid's reproductive potential.

Cockbain (1961b, c) has shown in the laboratory that flight capacity is directly related to the fat content within the alate aphid. He also showed that water loss during flight is not a limiting flight factor.

Broadbent (1949), working with Myzus persicae and Brevicoryne brassica, showed that light and in some cases humidity affected the activity of alate aphids. He observed that at a light intensity of 100-1000 foot candles, little difference in flight frequency resulted, but below 100 foot candles, activity declined rapidly. This work supports the work done with suction trap catches, explaining the low aphid populations at dusk, night, and at dawn (Lewis and Taylor, 1965). Kennedy and Booth (1963) stated that light is required to initiate, maintain and orient flight. In observations utilizing a free flight chamber, Kennedy observed that there appears to be an optimal light intensity for positive phototaxis; this phototaxis decreases until the aphid reaches exhaustion, when the phototaxis becomes negative.

In his laboratory work on the effect of humidity, Broadbent (1949) concluded that an increase in humidity temporarily retarded the aphid's activity, while a decrease in humidity increased activity. But the aphids soon adjusted and flew readily at all relative humidities between 50-100%. It was noted that a high humidity and a high temperature sometimes inhibited flight with Myzus persicae and Brevicoryne brassica. In conclusion Broadbent (1949) stated that changes in microclimate in crops are adequate to influence frequency of flight of aphids and consequently the spread of virus diseases.

The settling responses initiated after flight in Aphis fabae are quickly inhibited by an unsuitable host leaf (Kennedy and Booth, 1963).

If the alate aphid alights on an unsuitable host, it will soon take off, and repeat this behavior until a suitable host is found (B. Johnson, 1958).

In field experiments with Aphis fabae, Muller (1962) concluded that host selection apparently does not take place during the initial approach, but only after landing. The aphids took off sooner from non-hosts than from suitable host plants. The number of probes by the aphid on the non-host plant were about one, while probing on a suitable host was greater than one.

Kennedy and Booth (1963) concluded that settling is not released by flight but is positively primed while it is inhibited by flight, these two activities having been shown to be centrally antagonistic. The primary settling is given the name "antagonistic induction".

The strength of the settling response depends on three factors: the length of flight, the nature of the host plant surface, and the physical environment. It has been shown in Aphis fabae that a minimum flight from 10-20 seconds can be enough to elicit a settling response under certain conditions. Aphids flown for a few seconds and placed on seedlings in the light, settled and reproduced as did those on mature leaves in the dark. Those flown 30 minutes to 8 hours and placed on mature leaves in the light, probed and wandered but soon took off again (B. Johnson, 1958; Kennedy and Booth, 1963).

"Thus the complex of aphid flight behavior is in many species apparently attuned to one or a few short periods of flight and then a long sedentary reproduction phase" (Taylor, 1958).

Various factors other than flight have been found to elicit the settling response within alate aphids. Small doses of carbon dioxide were sufficient to affect the probing behavior in alate aphids (B. Johnson, 1958). Mutilation of the wings of Aphis fabae by pinching and twisting was seen to affect the settling responses by hastening reproduction (Chiang, 1960). It is also possible to elicit the settling response of an alate aphid by walking. But in the absence of flight, a longer period of activity occurred before the settling response was released (B. Johnson, 1958).

It is obvious that many factors affect the migrant status of alate aphids. The understanding of these factors and their interactions will lead to a broader knowledge of aphid migration and insect migration in general.

Materials and Methods

Cultures

Species of aphids used for testing.

1. Rhopalosiphum maidis (Fitch)
 - KS 1 - Cartier and Painter (1956)
 - KS 2 - Cartier and Painter (1956)
 - KS 3 - Pathak and Painter (1959)
 - KS 4 - Pathak and Painter (1959)
2. Rhopalosiphum fitchii (Sanderson)
3. Acyrtosiphon pisum (Harris)
4. Macrosiphum avenae (Kirby)

5. Aphis fabae (Scop.)

6. Schizaphis (=Toxoptera) graminum (Rondani)

Origin of test cultures.

Rhopalosiphum maidis

KS 1 - This clone was begun with a single apterous virginopara from the original culture established in 1954 by Cartier and Painter (1956) at Kansas State University by a single alate virginopara on White Martin sorghum.

KS 2 - This clone was begun by a single fourth instar alate virginopara from the culture established in 1954 by Cartier and Painter (1956) at Kansas State University by a single alate on sudan grass.

KS 3 - This clone was begun from a single virginopara from the culture established in 1956 by Pathak and Painter (1962) at Kansas State University from a colony collected on wheat.

KS 4 - This clone was begun from a single fourth instar apterous virginopara from the culture established in 1955 by Pathak and Painter (1962) from a single individual collected from barley.

Schizaphis (=Toxoptera) graminum - This clone was established from a single apterous virginopara from a mixed culture maintained by the Department of Entomology at Kansas State University.

Acyrtosiphon pisum - This clone was established from an apterous virginopara from a mixed culture maintained by the Department of Entomology at Kansas State University.

Macrosiphum avenae - This clone was begun with eight nymphs and adult virginoparae obtained from a mixed culture maintained by the Department of Plant Pathology at Kansas State University.

Rhopalosiphum fitchii - This clone was established from 30 apterous virginoparae obtained from a mixed culture maintained by the Department of Plant Pathology at Kansas State University.

Aphis fabae - This clone was established by 12 alate virginoparae sent by airplane from Rothamsted Experimental Station, Harpenden, Herts., England, from the original culture established in 1955 from a single apterous virginopara found on field beans. This strain of Aphis fabae was used by C. G. Johnson and Taylor (1957), and Taylor (1957), and Cockbain (1961a, b, c, d).

Experimental Materials

Culture cages. The culture cages as described by Dry (1965), were 18 inches wide, 18 inches deep, and 20 inches high. They had glass tops and doors and the sides and backs were of 50 inch x 50 inch lumite saran screen. The bottoms were of 1/4-inch plywood. The wooden frame was painted with three coats of white enamel to facilitate cleaning and maintenance of the cultures. Each culture cage held five 4 1/2 inch diameter pots in 6-inch clay saucers.

Plants. Barley was used as the host plant for R. maidis, R. fitchii, M. avenae, and S. graminum. Twenty Reno and Missouri Valley barley seeds

were planted in sterilized soil covered by one inch of white sand in 4 1/2-inch diameter pots. The pots were placed in clay saucers containing white sand to facilitate finding wandering aphids.

Broad beans, planted three to each 4 1/2-inch diameter pot in a similar manner to barley, were the host plant of A. pisum and A. fabae.

The barley and bean plants, isolated under a lumite screen to prevent contamination, were watered daily, and once a week were watered with a solution containing a fungicide (Captan) and a plant nutrient (Hyponex).

The culture plants were changed every 7-14 days. Twenty apterous aphids from the discarded culture were placed on new plants, 7-10 days old. Cages were cleaned, if necessary, at this time.

Regular planting maintained a supply of plants constantly through the testing period.

Observation cages. The observation cages were constructed of 8 1/2 x 11 inch cellulose acetate. This was formed into a cylinder 8 1/2 x 3 1/4 inches in diameter. Two 1-inch-square holes were cut in the side of the cage and covered with lumite screen. This enabled adequate ventilation and prevented condensation inside the observation cage. A top was placed on the cage made from a 4-inch embroidery hoop, covered with 50 x 50-inch lumite screen.

Greenhouse conditions. During the winter months the greenhouse was heated and the temperature was maintained at 20-25°C. During the spring and summer the greenhouse was cooled with cooling pads, exhaust fan, and three auxiliary bench fans. A layer of 4 mil polyethylene was stapled under the glass of the greenhouse roof to serve as a heat trap. Two layers of white shading compound were also applied to the roof. Control was still

difficult, and temperature recorded by a Cambridge recording thermograph ranged from 20-32°C.

The greenhouse was lit by six 250-watt incandescent bulbs.

Flight chamber. The chamber used for the dropping experiments was modified from the tethered flight chamber described by Cockbain (1961a). The frame was 44 inches long, 20 inches high and 20 inches wide; the top and sides were of 1/4-inch plexiglas; the front consisted of three removable plexiglas panels and a fourth panel was hinged to serve as a door. The bottom of the chamber was constructed of 1/2-inch plywood.

The chamber was heated by four 75-watt incandescent bulbs, each bulb wired separately. With this arrangement it was possible to keep a desired constant temperature by use of the lights and by removing the plexiglas panels.

For the free fall or dropping experiments, the chamber was turned on end. A hole was made at the top of the chamber. The aphids were dropped inside the chamber. The falling distance for the aphids was 37.5 inches from the hole to the bottom of the chamber (Fig. 1).

A thermometer was attached inside the chamber next to the dropping hole, to enable a constant check of the temperature to be made.

Experimental Methods

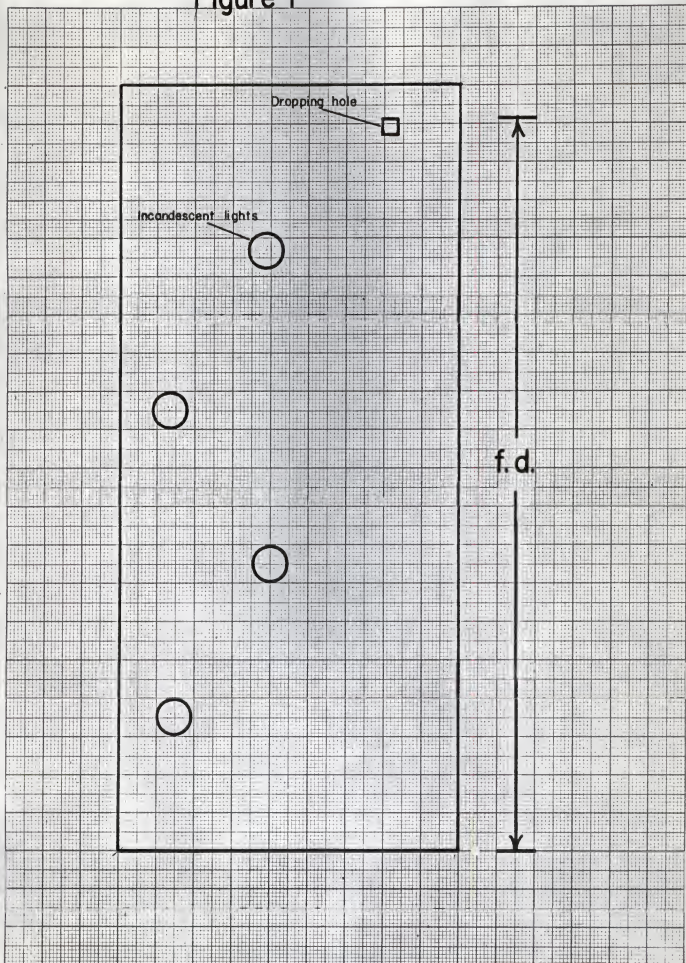
The flight response of an aphid to falling. The technique of dropping was employed to stimulate the flight responses of selected aphids. The technique is based on the concept of investigating thresholds for activity in populations as measured by the responses of individuals.

EXPLANATION OF FIGURE 1

A diagrammatic sketch of the modified flight chamber
used to test an aphid's flight response to falling.

f.d. equals falling distance of 37.5 inches.

Figure 1



An insect in flight, when subjected to cold or darkness will fold its wings and start to fall. The free fall technique seeks to measure the effects of various factors on the insect when it is in free fall.

By dropping an aphid it can be stimulated to fly in various ways. Such factors as inertia (Pringle, 1957), loss of tarsal contact (Frankel, 1932), the effect of wind on the head (Hollick, 1940; Weis-Fogh, 1956b), and changes in the relative position of the body (Diakonoff, 1936) are enough to initiate the flight response.

The falling responses of the aphids to various factors were presented graphically using the square root x-axis. The use of the square root x-axis presented a linear relationship and thus made the fitting of lines easier when applicable.

Pre-test preparation. Aphids were aspirated off the top of their culture cages the night before a test was to be set up. These aphids were discarded and the following morning the newly flown aphids were taken from the glass roof of the cage to insure uniform age and placed on their host plant.

The barley was thinned to 10-15 plants per pot. One alate aphid was then placed on each plant and an observation cage was placed over the barley plants. The barley plants and aphids were then placed in a Percival E-57 Environator (bench model, environmental chamber) and held at 20°C in darkness until the testing began. The relative humidity inside ranged from 50-70%.

Those aphids requiring broad beans for a host were placed on cuttings of broad bean in a bottle 2 1/4 inches tall and 1 inch in diameter, 2/3 full of water. The bean leaf was held in place by a cotton wad. A paper funnel around each cutting enabled any aphid that fell to return to its host.

The bottles were then placed in a pan 11 x 7 x 1 1/2 inches, filled with 1 inch of white sand. Five bottles were placed firmly in the sand of each pan, and 10-13 aphids were placed on each cutting. After infesting each cutting, the pans were quickly put into a refrigerator at 10°C. in darkness. The low temperature and lack of light prevented the aphids from wandering and falling off the plants. The aphids were held under these conditions until they were needed for testing.

All aphids used had been capable of flight since they had flown to the top of the culture cage where they were collected. Experiments were set up within three hours of this initial flight, assuming that no aphids were flying at night.

The effect of height on an aphid's response to flight. This experiment tested the validity of the free fall technique.

Aphids were obtained as previously described. They were then dropped in a Percival walk-in environmental chamber, with a height of 78 inches, more than twice that of the modified flight chamber.

The aphids were allowed to acclimatize to the dropping temperature for ten minutes before they were dropped. They were then dropped from a camel's-hair brush into the modified flight chamber. Twenty aphids were dropped each day, until all flight responses ceased. Those aphids that flew were recorded and the percentage that flew was obtained.

The light intensity at the dropping point in the walk-in chamber was approximately 2,000 foot candles.

The greenbugs were flown at 25°C. The temperatures used were based on the results of temperature response tests.

The effect of temperature on an aphid's flight response. The test aphids were set up in the manner already described. The greenbug and the

black bean aphid were held in the dark at 20°C. and 10°C., respectively. The holding temperatures insured an adequate temperature for reproduction to occur (Wadley, 1931; Daniels, 1963), but were well below the take-off and the flight thresholds determined by Dry (1965) and Cockbain (1961d).

Ten minutes previous to testing, the aphids were removed from the holding chambers and allowed to acclimatize to the temperature conditions that were being tested. The temperature range tested was from 15°C. - 40°C. Intervals of 5°C. were used for testing, and the percentage of aphids able to fly at each interval was recorded.

The aphids were removed from the host plant with a camel's-hair brush and then dropped in the modified flight chamber. The flight response was recorded and then the aphid was removed and destroyed.

Twenty aphids were dropped at each interval on successive days until no flight response was noted.

Each day of the testing the total number of nymphs produced by the alates was recorded.

The lighting in the modified flight chamber was produced by two G. E. 275-watt sun lamps. The light intensity in the chamber ranged from 1600-3200 foot candles, depending on the amount of sunlight entering the greenhouse.

The effect of light on an aphid's flight response. The purpose of this test was to determine if various light intensities had any inhibitory effect on aphids' response to being dropped. The test aphids were set up in the same manner as the temperature tests.

The aphids were removed from the holding chambers and allowed to acclimatize for ten minutes to the dropping conditions. These tests were

run at night to assure no interference of natural daylight. The light intensities used were 2,000, 200, 20, and 2 foot candles. A test was also run in what appeared to be complete darkness. The light intensities were measured with a Weston Model 756 Illumination Meter.

The various light intensities were obtained by using different combinations of lights and adjusting the distance of the lights from the dropping point. The combinations used were:

- 2,000 foot candles - 2 G. E. 275-watt sun lamps
- 200 foot candles - 1 150-watt incandescent light bulb
- 20 foot candles - 1 60-watt incandescent light bulb
- 2 foot candles - 6 night lights

Those which flew were recorded, and a percentage value for 20 aphids was recorded. The aphids were dropped every night until they no longer showed any flight response.

The temperature of dropping was maintained at 25°C. for the black bean aphid and 30°C. for the greenbug. The dropping temperatures were based on the temperature response tests.

The effect of starvation on an aphid's flight response. The aphids were collected from the tops of the culture cages and isolated individually in 4-dram vials. These vials were bound into groups of 20 and held in the dark as described in the previous tests. The aphids were dropped in the modified flight chamber with a camel's-hair brush. The greenbugs were dropped at 30°C. and the black bean aphid at 25°C.

Each group of 20 aphids was allowed to acclimatize to its dropping temperature for ten minutes. The aphids were then dropped at four-hour

intervals until the supply of test aphids was exhausted. The number that flew was recorded and a percentage value for those that flew was obtained.

The light intensity was maintained at 1600-2700 foot candles, with the use of two G. E. 275-watt sun lamps and the light present in the greenhouse.

Results and Discussion

General Observations

The responses of individuals were measured to gain an idea of the thresholds for activity in populations of aphids. The term response is used to denote the ability to respond by flight to falling.

The behavior of the aphid to falling is constant among the species tested. If the stimulus is adequate the aphid will fly in an upward or horizontal direction. The aphids tested early in their flying life appear more photo-positive and fly vertically to the ceiling of the chamber.

The aphids unable to fly fall to the floor of the chamber. Some of the aphids respond by flexing the wings while falling, while others leave them folded. Upon landing, the aphids characteristically flex their wings, fold them, and begin to wander.

Individual Flying Life Histories of S. graminum

If falling produces a stimulus for flight it is evident that the stimulus may vary in degree between species, between individuals, and between occasions. It is also evident that any variability can only be a reduction from an optimum stimulus, since overstimulation is not logically possible when the technique seeks to produce the maximum response. However, since the technique

may be imperfect, a normal response rather than an optimum response must be accepted and this may allow for a slight increase in responses in certain circumstances. This is shown in Plate III where the super-stimulus of 35-40°C. in A. fabae produced a response almost entirely restricted to the upper edge of the 95% confidence limit line.

Because insects sometimes fail to respond as expected, any single failure of an aphid to fly may not mean a complete loss of ability to fly by that aphid.

To determine the variability within individuals the flight responses of 20 greenbugs were tested every 10 minutes for an hour and again at two hours after initial flight. The flight responses were recorded as "+" for flight and "-" for no flight response (Table 1).

If a perfect technique were used and a perfect response to stimulus obtained, the individual's flight response would be: ++++----, ++----- or ++++++--, but the technique is not perfect and variability in response by the same individual occurs on successive occasions (Table 1). It was not possible to investigate the individual histories in the other experiments, since they were done on a group basis, but this special series was done on the greenbug to point out the variability in the technique and the variability that exists within an aphid species.

The Effect of Height on Free Fall

Since free fall responses were the basis of the proposed study, it was necessary to see if height inside the modified flight chamber was adequate to stimulate flight in A. fabae and S. graminum.

TABLE 1. The individual flying life histories of *S. graminum* held at 20°C., dropped at 30°C. in light exceeding 2000 foot candles.

Aphid Number	Minutes							
	0	10	20	30	40	50	60	120
1	+	+	+	-	-	+	+	+
2	+	+	+	-	+	+	+	+
3	+	+	+	+	+	-	+	+
4	+	+	+	+	+	+	+	+
5	+	+	+	+	+	+	+	+
6	+	+	+	+	+	+	+	+
7	+	+	+	+	+	+	+	-
8	+	+	-	-	+	+	+	-
9	+	+	+	+	+	+	+	+
10	+	+	+	+	-	-	-	-
11	+	+	-	-	+	-	-	+
12	+	+	+	+	+	+	+	+
13	+	+	+	-	+	-	-	-
14	+	+	-	+	-	+	+	-
15	+	+	+	+	+	+	+	+
16	+	+	+	+	+	+	+	+
17	+	+	+	-	-	+	+	-
18	+	+	+	+	+	+	+	+
19	+	+	-	-	-	+	-	-
20	+	+	+	-	-	-	-	-
Number of +'s	20	20	16	12	14	15	15	12
Number of -'s	0	0	4	8	6	5	5	8
% flight response	100	100	80	60	70	75	75	60

+ equals flight response

- equals no flight response

The modified flight chamber offered a distance of 37.5 inches in which the aphids had the opportunity to respond to the falling stimulus. As a comparison, a walk-in environmental chamber with a height of 78 inches was used. The aphids were held and dropped under similar conditions, as previously described.

S. graminum (Plate I) showed a flight response over a falling distance of 78 inches at 30°C. intermediate between the response elicited over a 37.5 inch fall, at 25°C. and 30°C. The close similarity between these regression lines indicates that between 37.5 inches, and 78 inches, height had little effect on the flight responses of S. graminum.

The flight responses elicited in A. fabae (Plate II) shows that the regression lines for all measurements are so similar that only one common line can be drawn. It is apparent that the dropping height had no effect on the flight response of A. fabae.

It therefore appears that, since doubling the falling distance produced no increase in the flight response, the distance originally chosen, 37.5 inches, is adequate for the purpose of stimulating flight.

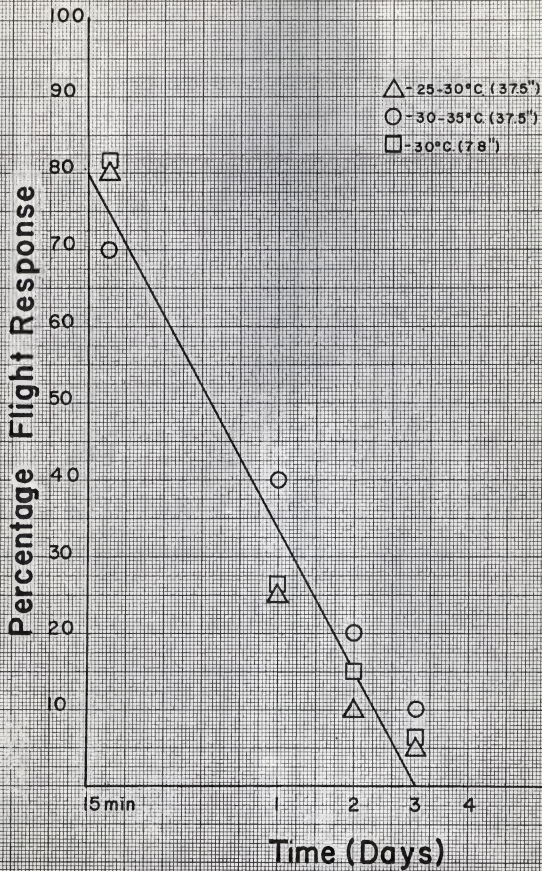
The Effect of Temperature on an Aphid's Flight Response

Temperature is a factor known to influence the pre-migrant status as well as the migrant status of an aphid (Wellington, 1945; Taylor, 1957, 1963). In the present study it was found that temperature had a direct effect on an aphid's flight responses (Plates III and IV).

In the black bean aphid there was no distinguishable effect of temperature from the range of 15-40°C., 15 minutes after the first flight. At temperatures below 15°C. the aphids would not respond to the stimulus and

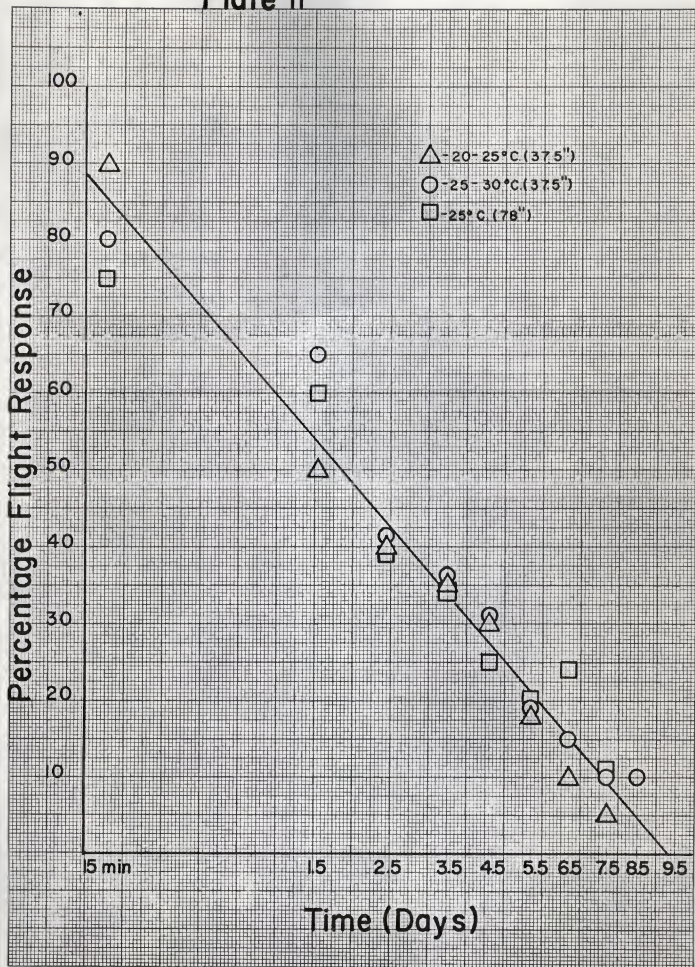
EXPLANATION OF PLATE I

The effect of height on the flight responses of S. graminum held at 20°C. and dropped in light exceeding 2,000 foot candles. Percentage points based on the responses of 20 aphids and plotted on a square root scale to obtain a straight line distribution. Eye-fitted regression line.



EXPLANATION OF PLATE II

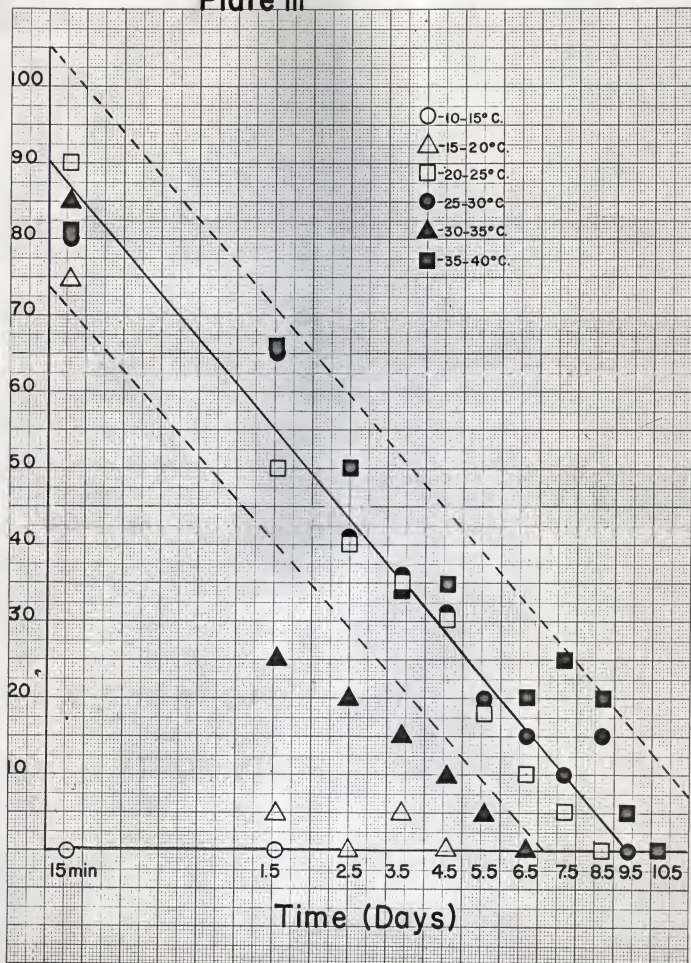
The effect of height on the flight responses of A. fabae held at 10°C. and dropped in light exceeding 2,000 foot candles. Percentage points based on the responses of 20 aphids and plotted on a square root scale to obtain a straight line distribution. Eye-fitted regression line.



EXPLANATION OF PLATE III

The effect of temperature on the flight responses of A. fabae held at 10°C. and dropped in light exceeding 2,000 foot candles. Percentage points based on the responses of 20 aphids and plotted on a square root scale to obtain a straight line distribution. Dotted lines represent 95% fitted confidence limits with a fitted mean.

Percentage Flight Response



EXPLANATION OF PLATE IV

The effect of temperature on the flight responses of S. graminum held at 20°C. and dropped in light exceeding 2,000 foot candles. Percentage points based on the responses of 20 aphids and plotted on a square root scale to obtain a straight line distribution. Dotted lines represent 95% fitted confidence limits with a fitted mean.

Plate IV

Percentage Flight Response

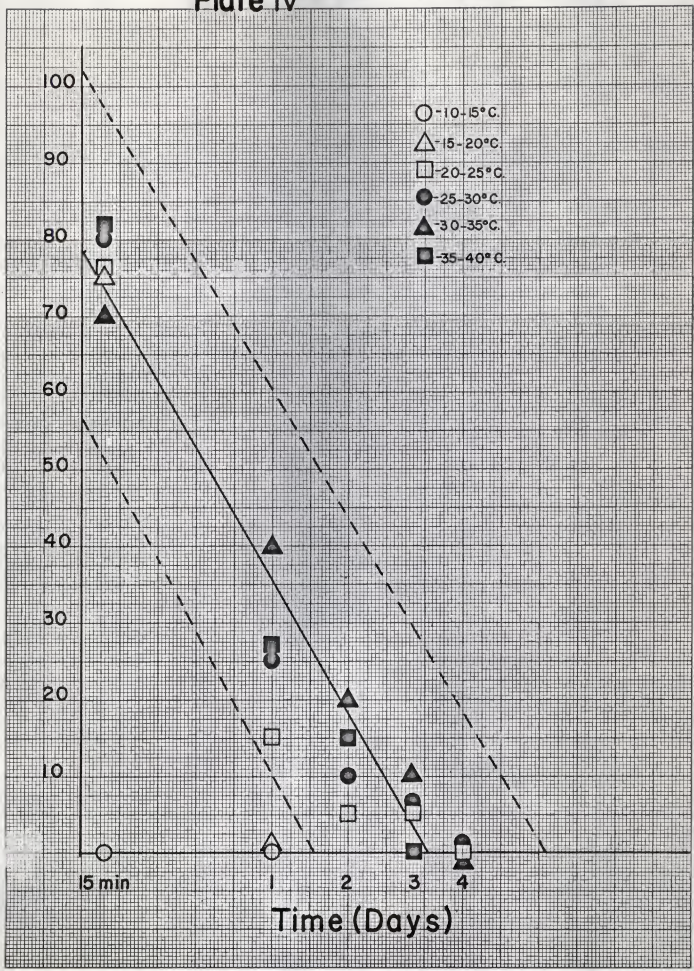
100
90
80
70
60
50
40
30
20
10

5 min

Time (Days)

- - 10-15°C.
- △ - 15-20°C.
- - 20-25°C.
- - 25-30°C.
- ▲ - 30-35°C.
- - 35-40°C.

1 2 3 4



invariably fell with their wings folded. Wellington (1945) noted that an insect folded its wings when subjected to temperatures below its flight threshold.

After 36 hours, the inhibition of the flight response is noted at temperatures between 15-20°C. A normal response is given for temperatures between 20-30°C. and 35-40°C. At temperatures between 30-35°C. the flight response begins to decrease and eventually drops far short of the normal responses. This drop could be attributed to a lack of stimulus at temperatures between 30-35°C.

It appears that only low temperatures below 15°C. prevent flight. Flight limitation can be seen at temperatures from 15-20°C. and 30-35°C. The normal response temperatures for flight response appear to be in the range of 20-30°C. The apparently normal responses elicited at the 35-40°C. range can be attributed to a near death response by the aphid nearing its thermal death point, which has been demonstrated in several insect species.

The greenbug's response to temperature at the 15 minute point is similar to the black bean aphid's response. At temperatures of 15-40°C. no inhibition of the flight response occurs, but below 15°C. the flight response is prevented.

After one day, the flight responses of the greenbugs tested were normal at temperatures between 20-40°C. Inhibition of the flight responses occurred at temperatures below 20°C. The normal responses in the 20-40°C. range were maintained until cessation of the flight responses at the end of four days.

The differences between the black bean aphid's and the greenbug's responses to temperature are evident. The black bean aphid will fly for

more days than the greenbug throughout the entire range of flight temperatures. The apparent simplicity of the greenbug's response to temperature is in contrast to the observed complexity of the black bean aphid's response. The black bean aphid appears to have a response gradient, while the greenbug either did not fly or had a normal flight response.

The Effect of Light on an Aphid's Flight Response

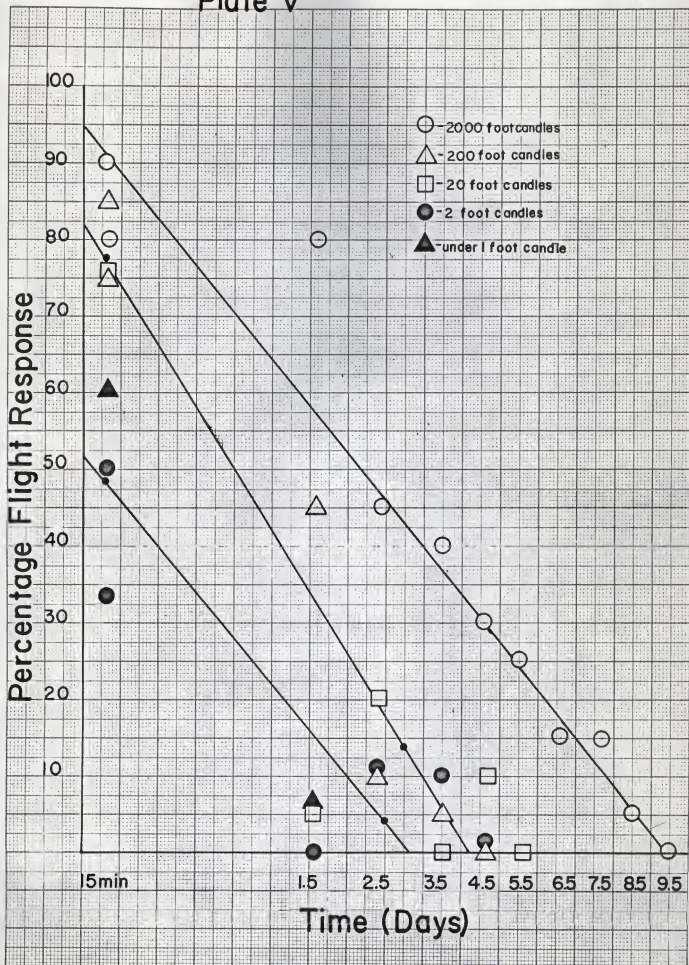
Light is known to be a limiting factor in an aphid's pre-migrant behavior as well as in its subsequent migrant behavior. In the present study the effect of light was found to be a limiting factor on the flight responses of the aphids tested.

A. fabae had its maximum response at 2,000 foot candles, from 15 minutes until the cessation of the flight response at 9.5 days. A mean line was drawn for the moderate responses to show the deviation from the responses at low light intensities (Plate V). At light intensities of 200 foot candles and 20 foot candles the aphids showed a moderate response. At 15 minutes they behaved as at 2,000 foot candles, but after 1.5 days, the flight response deviates from the normal and ceases at 4 days, in contrast to 9.5 days for those flown at 2,000 foot candles. Aphids dropped at 2 foot candles responded poorly. At 15 minutes only about 50% responded, and this declined until the mean cessation of the flight response at low light intensities terminated at approximately 3 days.

S. graminum shows a maximum flight response at 2,000 foot candles. At light intensities below 2,000 foot candles there appears to be a sub-normal response. At 200, 20, 2, and below 1 foot candle the aphids seem to respond

EXPLANATION OF PLATE V

The effect of light on the flight responses of A. fabae held at 10°C. and dropped at 25°C. Percentage points based on the responses of 20 aphids and plotted on a square root scale to obtain a straight line distribution. Fitted mean lines with reference points.



poorly. The gradient among the flight responses of S. graminum at low light intensities is not as pronounced as that found in A. fabae (Plate VI).

The Effect of Starvation on an Aphid's Flight Response

The migrant status of an aphid is known to be affected by starvation. Cockbain (1961c) showed that A. fabae flown tethered until exhaustion, lived for a significantly shorter time than those starved without flight. In the present study the effect of starvation on the aphid's flight responses was compared with the flight responses given under normal conditions.

The effect of starvation in the first 12 hours of flying life does not appear to affect the flight responses of the greenbug or the black bean aphid (Plates VII and VIII).

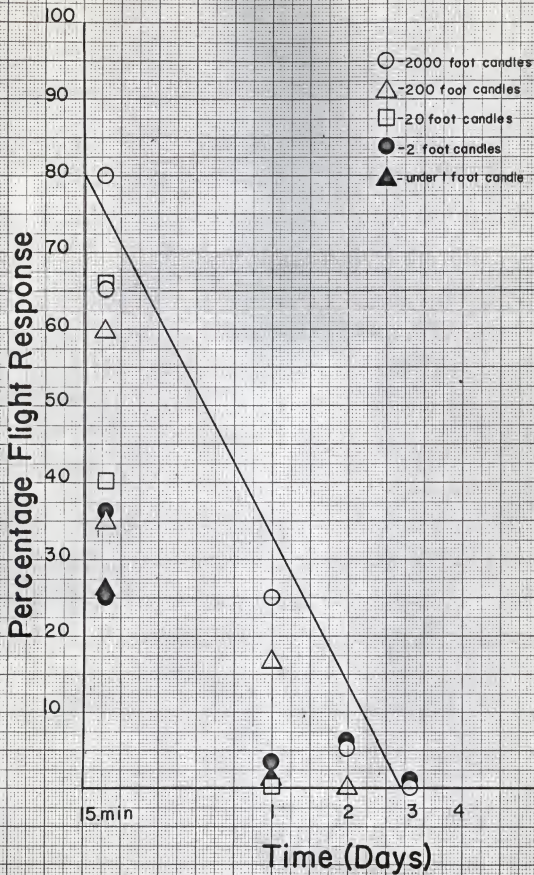
After 12 hours the black bean aphid's flight responses begin to deviate from the normal responses. The deviation continues until cessation of the flight response of the starved aphids which occurs at 3.5 days. The non-starved, black bean aphids continue to respond until 9.5 days.

The greenbug shows a deviation in flight response similar to the black bean aphid's after the first 12 hours of starvation. The deviation continues until the cessation of the flight response at 1.83 days. The nonstarved greenbugs continue the flight response until cessation occurs at 3 days.

It is quite evident that lack of food is a flight limiting factor in the aphids tested. The initial lack of food is not a noticeable hindrance, but the effect of time and starvation appears after 0.5 days, and the aphid's ability to respond to the flight stimulus subsequently decreases.

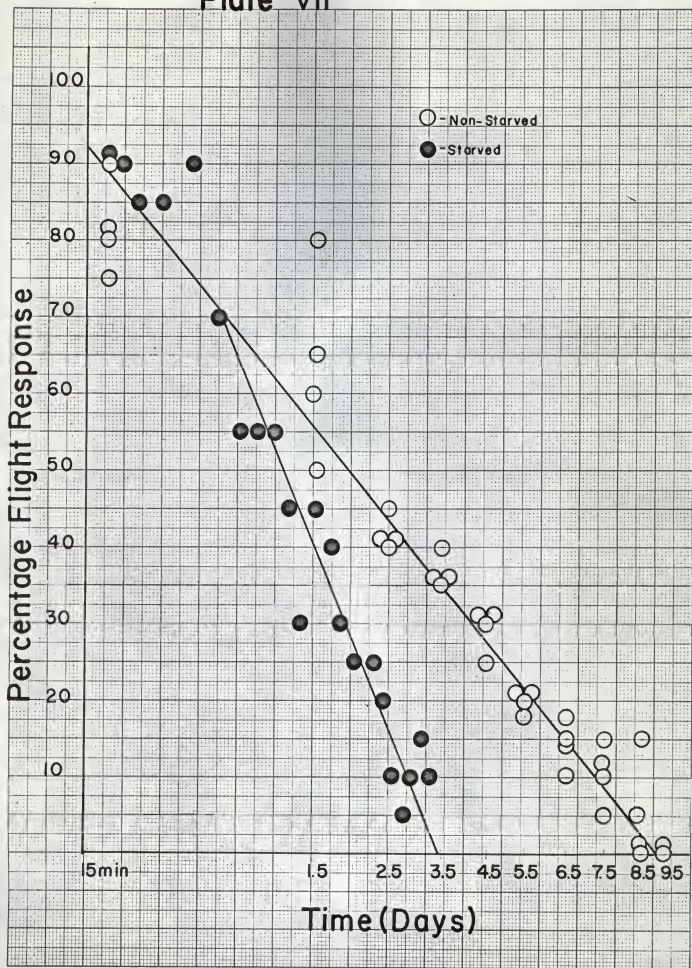
EXPLANATION OF PLATE VI

The effect of light on the flight responses of S. graminum held at 20°C. and dropped at 30°C. Percentage points based on the responses of 20 aphids and plotted on a square root scale to obtain a straight line distribution. Eye fitted lines.



EXPLANATION OF PLATE VII

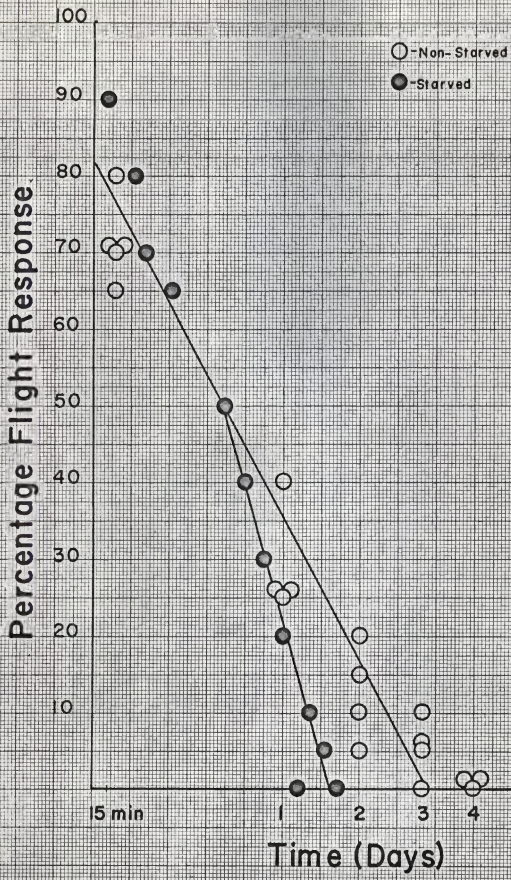
The effect of starvation on the flight responses of A. fabae held at 10°C. and dropped in light exceeding 2,000 foot candles. Percentage points based on the responses of 20 aphids and plotted on a square root scale to obtain a straight line distribution. Lines eye fitted.



EXPLANATION OF PLATE VIII

The effect of starvation on the flight responses of S. graminum held at 20°C. and dropped in light exceeding 2,000 foot candles. Percentage points based on the responses of 20 aphids and plotted on a square root scale to obtain a straight line distribution. Lines eye fitted.

Plate VIII



Length of Flying Life of an Aphid

Plate IX is a graphic representation of the length of an aphid's flying life, showing differences at the species level and, in the case of the corn leaf aphid, at the infrasubspecific level.

The ability to respond to the falling stimulus was plotted against time in the aphid's flying life.

At the 50% point, differences among the aphids to respond to falling become clearer. The corn leaf aphid biotypes maintain their ability to respond to a greater extent than does the apple grain aphid and the English grain aphid.

At the 5% point, three of the corn leaf aphid biotypes have separated from the other species or biotypes, but are similar in their response. The English grain aphid and KS-4 appear to be similar in their first 36 hours of flying life, but KS-4 maintains the ability to fly 24 hours longer than the English grain aphid. The apple grain aphid appears to be the least responsive of the aphids tested, with the exception of the pea aphid. Its flying life is limited to the first 36 hours after initial flight, while the pea aphid shows no response after 15 minutes.

The corn leaf aphid biotypes as separated originally by Painter, Cartier, and Pathak (1956, 1959) fall into three groups on the basis of flying life. KS-3 and KS-4 appear to be at the two extremes, with KS-3 flying longer; KS-1 and KS-2 are similar and fall between KS-3 and KS-4; and KS-4 have the shortest flying life.

EXPLANATION OF PLATE IX

The length of flying life of M. avenae, R. fitchii,
A. pisum, and the biotypes of R. maidis. Percentage
points based on the responses of 20 aphids and plotted
on probability paper. Lines eye fitted.

Plate IX

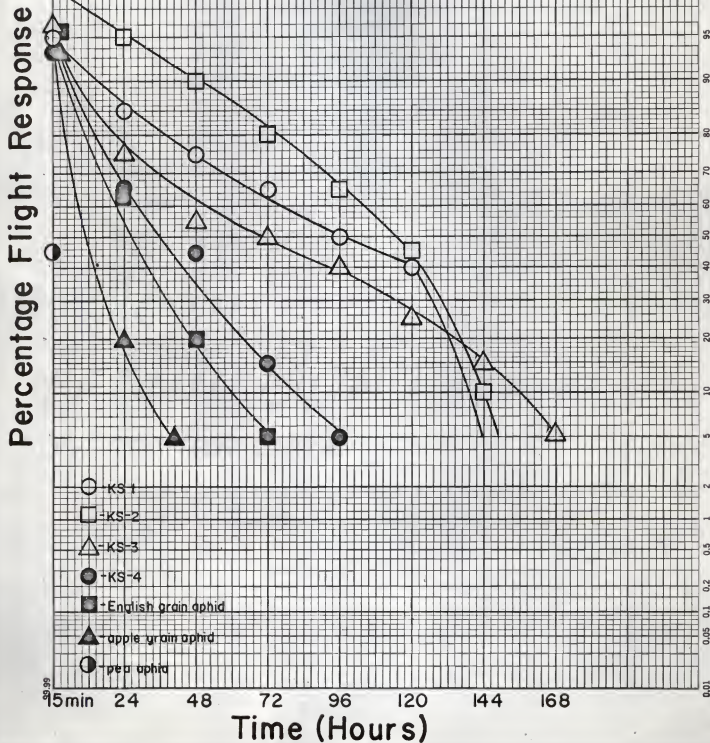


TABLE 2. The length of flying life of M. avenae, R. fitchii and the biotypes of R. maidis at various flight response levels.

Flight response level	<u>M. avenae</u>	<u>R. fitchii</u>	<u>R. maidis</u>			
			KS-1	KS-2	KS-3	KS-4
95%	0.25 hr	0.25 hr	0.25 hr	24 hr	0.25 hr	0.25 hr
50%	33 hr	12 hr	96 hr	115 hr	67 hr	36 hr
.05%	72 hr	41 hr	144 hr	149 hr	168 hr	96 hr

Aphid Reproduction at Various Ages

The reproductive ability of the aphids at different ages was observed in association with the experiments on length of flying life. The pea aphid and the apple grain aphid have relatively short flying lives; as a result the reproduction data obtained from them are limited (Plate XI). All English grain aphids were reproducing after 2 days and 50% of pea aphids after 3 days.

Within biotypes of the corn leaf aphid, 95% of KS-3 and 87% of KS-1 were reproducing by the end of the eighth day; 48% of KS-2 at the end of the seventh day; and 20-25% of KS-4 at the end of the fifth day. In no biotype did 100% of the aphids reproduce every day (Plate X).

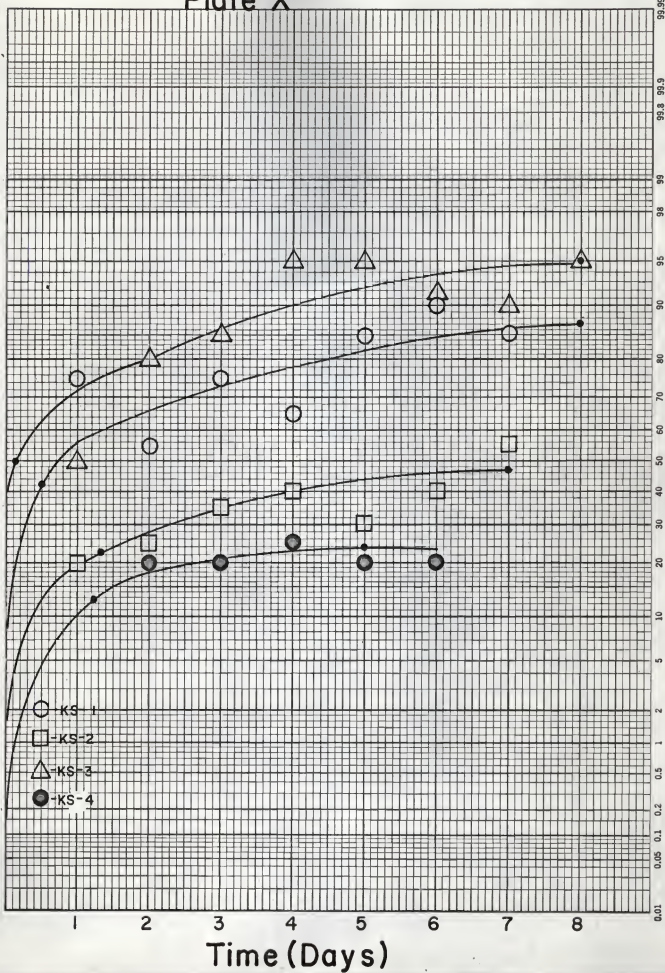
Fifty percent of the maximum rate of reproduction of KS-3 was reached in 0.15 days; 0.5 days in KS-1; 1.2 days in KS-2 and 1.1 days in KS-4. KS-1 and KS-3, therefore, not only had the highest rate of reproduction, but also reached their maximum earlier.

EXPLANATION OF PLATE X

Reproduction at various ages by the biotypes of
R. maidis. Percentage points based on the responses
of 20 aphids and plotted on probability paper with
reference points. Lines eye fitted.

Plate X

Percent Reproducing



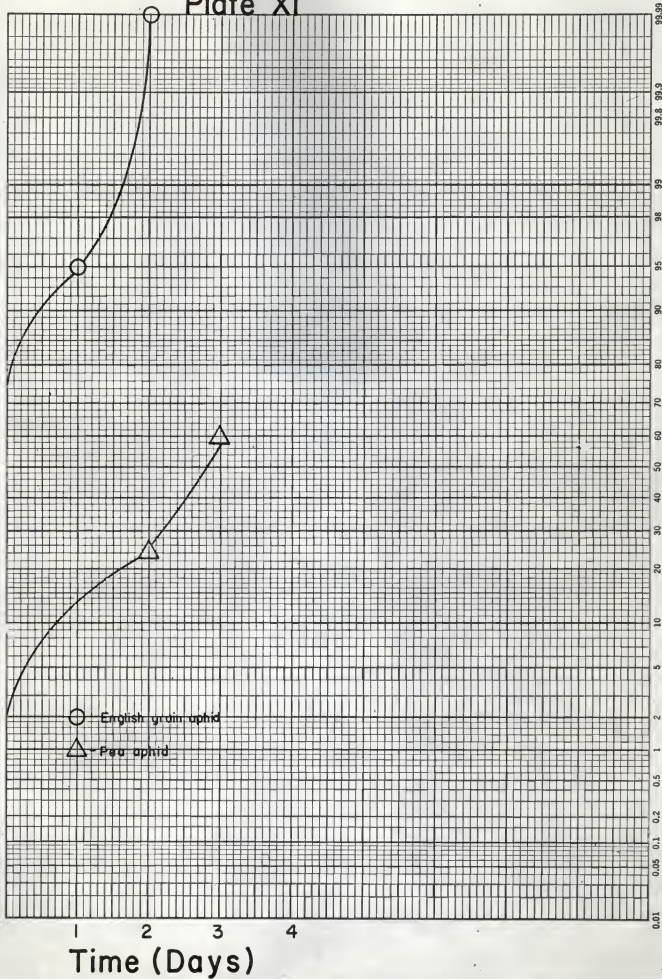
Time (Days)

EXPLANATION OF PLATE XI

Reproduction at various ages by M. avenae and S. pisum.
Percentage points based on 20 aphids and plotted on proba-
bility paper. Lines eye fitted.

Plate XI

Percent Reproducing



The greenbug appears to possess the greatest reproductive ability. By the end of the second day of its flying life it had nearly reached its maximum rate of reproduction of 100% (Table 3). The reproductive ability of the greenbug appears to stabilize at nearly 100% at least through the first five days of flying life.

The black bean aphid shows a gradual increase in rate of reproduction. The increase is evident up to 7.5 days, when 80% of the aphids observed had reproduced (Table 4). The subsequent drop in reproduction can be accounted for by the condition of the host plant used for observing the reproductive behavior. These aphids were placed on basal leaves of the broad bean rather than apical leaves as was done for the first 7.5 days of observation.

The Relationship between Length of Flying Life and Reproduction

The intraspecific relationship between length of flying life and reproduction in the corn leaf aphid appears to be a direct one. KS-3 has the greatest fecundity and the greatest length of flying life. At the other extreme, KS-4 has the shortest flying life and the least amount of reproduction. KS-1 and KS-2 fall between KS-3 and KS-4 in both flying life and fecundity.

It is evident that the interspecific relationship between length of flying life and fecundity is not direct. The greenbug, a relatively poor flier, reaches its maximum reproduction by the end of the second day.

The English grain aphid reaches 100% reproduction at the end of the second day, while its flying life extends to 72 hours.

TABLE 3. Reproduction at various ages in *S. graminum* held at 20°C. Percent reproducing based on 20 aphids done simultaneously with temperature experiments.

Day	Number reproducing					% reproducing
15 min	0	0	0	0	0	0
1	20	20	20	20	19	99.0
2	20	20	20	20	18	98.0
3	20	20	20	20	20	100.0
4	20	20	20	20	20	100.0
5	20	20	20	20	20	100.0

TABLE 4. Reproduction at various ages in *A. fabae* held at 10°C. Percent reproducing based on 20 aphids done simultaneously with temperature experiments.

Day	Number reproducing					% reproducing
15 min	0	0	0	0	0	0
1.5	1	11	2	1	4	24.2
2.5	12	12	10	7	13	45.0
3.5	13	10	15	10	9	48.5
4.5	13	16	11	12	15	55.5
5.5	12	26*	15	13	7	50.5
6.5	-	15	15	14	14	72.5
7.5	-	15	15	-	14	80.0
8.5	-	15	9	-	15	66.0
9.5	-	-	8	-	-	40.0
10.5	-	-	10	-	-	50.0

* Based on 40 aphids.

The black bean aphid, appearing to be a strong flier in comparison to the other pest aphids tested, shows a gradual increase in reproduction as time increases. Bruce Johnson (1957) found that A. fabae, flown for one hour in tethered flight produced an average of 12 nymphs the first day, and averaged four nymphs per day for the following three days. It seems likely that if the aphids tested in the present study would have had more flight to stimulate the settling response, the reproduction would have been greater. The lack of initial flight may have affected the subsequent reproductive ability. Observations on all the aphids tested tend to indicate that complete cessation of the flight response is not a prerequisite to reproduction.

Bruce Johnson (1957) found that a number of aphids including Sappaphis mali, Aphis fabae, Brevicoryne brassicae, Myzus persicae, and Macrosiphum euphorbiae had the ability to reproduce before the ability to fly was lost. He attributed this reproduction to embryos formed before the arresting of the embryo development that occurs after the end of the teneral period.

The reproduction in the aphids tested indicates that there must be a number of fully formed embryos within the alate aphids before the initial flight occurs. Muscle autolysis must not be essential for reproduction to start, but it may be necessary for reproduction to continue. A study of the histology of muscle autolysis in the aphids tested would give a clearer understanding of the results obtained.

Summary and Conclusions

The intraspecific variability of the test aphids was noted by observing the flight responses of greenbugs at specific intervals. It was

determined that individual variability within an aphid species does exist, and that aphids capable of flying do not always fly under usual flight conditions.

The results comparing dropping distances of 37.5 and 78 inches indicate that doubling the falling distance did not increase the flight response.

A. fabae showed a comparatively complex response to temperature, while S. graminum was observed to react in a less complex manner. A. fabae did not fly at temperatures below 15°C. At 15-20°C. and 30-35°C. a poor response was elicited; at 35-40°C. a supernormal response was seen; and from 20-30°C. the aphids responded normally.† It is evident that temperature is a flight limiting factor and influences the over-all migratory status of alate aphids.

At a light intensity of 2,000 foot candles, both A. fabae and S. graminum responded normally. Below 2,000 foot candles response diminished for both aphids tested. A. fabae responded moderately at 200 foot candles and 20 foot candles and poorly at and below 2 foot candles. S. graminum appears to show a subnormal response at all intensities below 2,000 foot candles. The deviations are not as distinct as in A. fabae and cannot be separated in such a clear-cut fashion. It is obvious that both A. fabae and S. graminum will respond to the flight stimulus at low light intensities, at least in their early flying life. A low light intensity is a flight limiting factor, but this does not discount the possibility that an aphid in flight could possibly maintain its flight at intensities too low to initiate flight. It is believed that an aphid, when subjected to low temperatures or darkness, will fold its wings and begin to fall. It is possible that the falling of the aphid may elicit enough of a flight stimulus,

in proper conditions, to resume flight. This implication could account for the longer range migrations where the aphid would have to be flying at night.

Starvation of A. fabae and S. graminum was observed to affect the flight responses after 0.5 days; both A. fabae and S. graminum responded less than when fed, until the starved aphids ceased to respond at 3.5 and 1.83 days, respectively. The normal nonstarved A. fabae and S. graminum continued to respond to the flight stimulus for 9 and 3 days, respectively (Plate XII). These observations tend to indicate that starvation begins to affect the aphid's flight responses after 0.5 days. Without the presence of adequate food the aphids tested readily lost their ability to respond to the flight stimulus.

To gain an accurate idea of an aphid's migratory ability it is necessary to determine the length of its flying life. If an aphid's flying life is short it is reasonable to assume that any migration must be completed in one hop. There are many factors that may limit migration time, among these are: "willingness" of an aphid to fly, inhibition by adverse conditions, exhaustion of immediate reserves, exhaustion of total reserves, muscle autolysis, and death. Tests were carried out to determine the length of flying life of certain pest aphids. It was found that there is a definite difference in the length of flying life between species and in the case of the corn leaf aphid between biotypes. It was found that KS-3 had the greatest flying life, 5% maintaining the flight response through 168 hours, while KS-4 showed the least ability, 5% maintaining the flight response for only 96 hours. KS-1 and KS-2 showed an intermediate

EXPLANATION OF PLATE XII

The effect of starvation on the flight responses of A. fabae
and S. graminum. Plotted on a transformed square root scale.

Plate XII

Percentage Flight Response

A fabae
S. graminum

Time (Days)

9

8

7

6

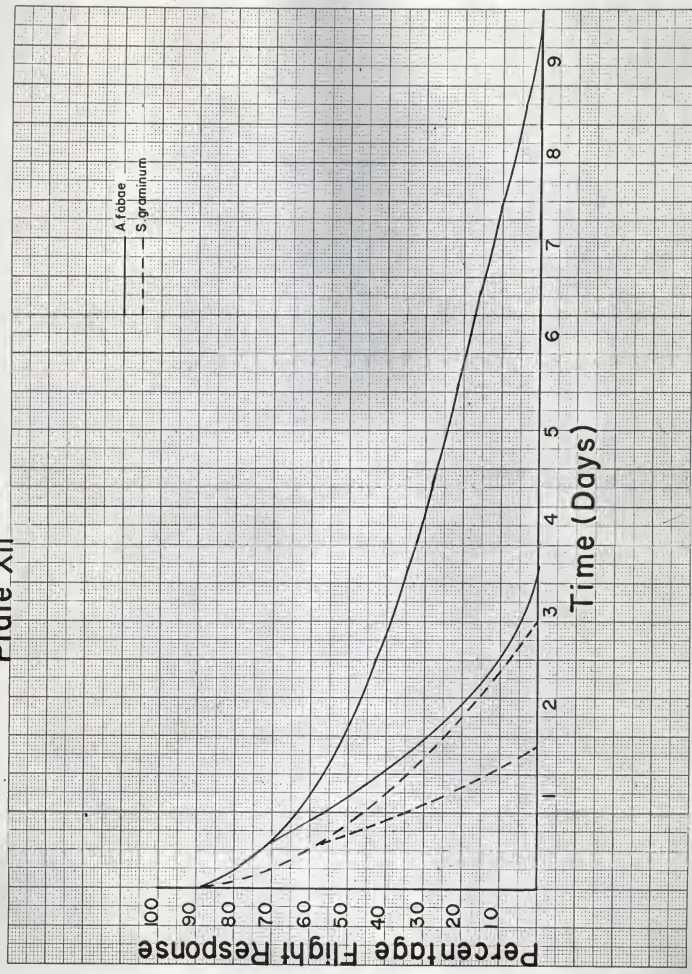
5

4

3

2

1



length in flying life, their responses being in between KS-3 and KS-4. The English grain aphid lost its ability to fly after 72 hours, the apple grain aphid after 24 hours, and the pea aphid after 15 minutes.

Reproduction differences were noted for all the aphids tested. All of the aphids tested were capable of reproduction before the cessation of the flight response. The biotypes of the corn leaf aphid varied greatly in their ability to reproduce. KS-3 showed the greatest fecundity, KS-4 the lowest, with KS-1 and KS-2 intermediate in their ability to reproduce. The highest rates of reproduction were seen in the greenbug and the English grain aphid, which reached maximum reproduction at the end of the second day of their flying life. The black bean aphid showed a gradual rate of reproductive increase, reaching its highest rate at the end of 7.5 days. The subsequent drop in reproduction can be attributed to the change in the condition of the culture plant.

The relationship between length of flying life and reproduction appears to be species specific. In the biotypes of the corn leaf aphid, the most responsive biotypes possessed the greatest reproductive capacity. Comparatively poor fliers like the English grain aphid and the greenbug reached 100% reproduction by the end of the second day. It is evident that the relationship between length of flying life and reproduction is complex, but it appears that the reproductive ability is so geared that a migrant aphid could easily settle and begin reproduction with a minimum of flight. These observations show that aphid migration is not compulsive and that the need for an aphid species to migrate is less once reproduction has begun. The economic implications are obvious, a migratory aphid could alight and begin reproduction and in a short period of time could cause serious damage to crops by its feeding and by the spread of virus diseases.

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APPENDIX

TABLE 5. The effect of height on the flight responses of S. graminum. Percentage flight response based on the responses of twenty aphids.

Temperature	Height	15 min	Days			
			1	2	3	4
25-30°C.	37.5"	.60	.25	.10	.05	0
30-35°C.	37.5"	.70	.40	.20	.10	0
30°C.	78"	.80	.25	.15	.05	0

TABLE 6. The effect of height on the flight responses of A. fabae. Percentage flight response based on the responses of twenty aphids.

Temperature	Height	15 min	Days									
			1.5	2.5	3.5	4.5	5.5	6.5	7.5	8.5	9.5	
20-25°C.	37.5"	.90	.50	.40	.35	.30	.18	.10	.05	0	-	
25-30°C.	37.5"	.80	.65	.40	.35	.30	.20	.15	.10	.10	0	
25°C.	78"	.75	.60	.40	.35	.25	.20	.24	.10	0	-	

TABLE 7. The effect of temperature on the flight responses of *E. graminum*, held at 20°C. and dropped in light exceeding 2000 foot candles. Percentage flight response based on twenty aphids.

Temperature	15 min	Days			
		1	2	3	4
10-15°C.	0	0	-	-	-
15-20°C.	.75	0	-	-	-
20-25°C.	.75	.15	.05	.05	0
25-30°C.	.80	.25	.10	.05	0
30-35°C.	.70	.40	.20	.10	0
35-40°C.	.80	.25	.15	0	-

TABLE 8. The effect of temperature on the flight responses of *A. fabae* held at 10°C. and dropped in light exceeding 2000 foot candles. Percentage flight response based on twenty aphids.

Temperature	15 min	Days									
		1.5	2.5	3.5	4.5	5.5	6.5	7.5	8.5	9.5	10.5
10-15°C.	0	0	-	-	-	-	-	-	-	-	-
15-20°C.	.75	.05	0	.05	0	-	-	-	-	-	-
20-25°C.	.90	.50	.40	.35	.30	.18	.10	.05	0	-	-
25-30°C.	.80	.65	.40	.35	.30	.20	.15	.10	.15	0	-
30-35°C.	.85	.25	.20	.15	.10	.05	0	-	-	-	-
35-40°C.	.80	.65	.50	.35	.35	.20	.20	.25	.20	.05	0

TABLE 9. The effect of light on the flight responses of *S. graminum*, held at 20°C. and dropped at 30°C. Percentage flight response based on the responses of twenty aphids.

Light intensity	15 min	Days			
		1	2	3	4
2000 foot candles	.65 .80	.25	.05	0	-
200 foot candles	.60 .35	.16	0	-	-
20 foot candles	.65 .40	0	-	-	-
2 foot candles	.35 .25	0	.05	0	-
under 1 foot candle	.25	0	-	-	-

TABLE 10. The effect of light on the flight responses of *A. fabae* held at 10°C. and dropped at 25°C. Percentage flight response based on the responses of twenty aphids.

Light intensity	15min	Days								
		1.5	2.5	3.5	4.5	5.5	6.5	7.5	8.5	9.5
2000 foot candles	.90 .80	.80	.45	.40	.30	.25	.15	.15	.05	0
200 foot candles	.85 .75	.45	.10	.05	0	-	-	-	-	-
20 foot candles	.75 .75	.05	.20	0	.10	0	-	-	-	-
2 foot candles	.35 .50	0	.10	.10	0	-	-	-	-	-
under 1 foot candle	.60	.05	0	-	-	-	-	-	-	-

TABLE 11. The effect of starvation on the flight responses of *S. graminum*, held at 20°C. and dropped at 30°C. in light exceeding 2000 foot candles. Percentage flight response based on the responses of twenty aphids.

15min	Hours												
	1	2	4	8	12	16	20	24	28	32	36	40	44
.90	.80	.70	.65	.65	.50	.40	.30	.20	0	.10	.05	0	0

TABLE 12. The effect of starvation on the flight responses of *A. fabae*, held at 10°C. and dropped at 25°C. in light exceeding 2000 foot candles. Percentage flight response based on the responses of twenty aphids.

15min	Hours												
	1	2	4	8	12	16	20	24	28	32	36	40	44
.90	.90	.85	.85	.90	.70	.55	.55	.55	.45	.30	.45	.40	.30

Hours									
48	52	56	60	64	68	72	76	80	
.25	.45	.25	.20	.10	.05	.10	.15	.10	

TABLE 13. The effect of time on the flight responses of selected aphids. Percentage flight response based on the responses of twenty aphids held at greenhouse temperature in the dark.

Species	Strain	Dropping Temp. °C.	Hours								
			.25	24	48	72	96	120	144	168	192
R. maidis	KS-1	30-35	.95	.85	.75	.65	.50	.40	0	-	-
R. maidis	KS-2	30-35	100	.95	.90	.80	.65	.45	.10	0	-
R. maidis	KS-3	30-35	.95	.75	.55	.50	.40	.25	.15	.05	0
R. maidis	KS-4	30-35	.95	.65	.45	.15	.05	0	-	-	-
R. fitchii	Lab	30-35	.95	.20	0	-	-	-	-	-	-
M. avenae	Lab	25-28	.95	.65	.20	.05	0	-	-	-	-
A. pisum	Lab	30-35	.55	0	-	-	-	-	-	-	-

TABLE 14. The reproduction of selected aphids at various ages. Percentage reproduced based on the observation of twenty aphids held at greenhouse temperature in the dark.

Species	Strain	Hours								
		.25	24	48	72	96	120	144	168	192
R. maidis	KS-1	0	.75	.55	.75	.65	.85	.90	.85	-
R. maidis	KS-2	0	.20	.25	.35	.40	.30	.40	.55	-
R. maidis	KS-3	0	.50	.80	.85	.95	.95	.90	.90	.95
R. maidis	KS-4	0	0	.20	.20	.25	.20	.20	-	-
R. fitchii	Lab	0	0	-	-	-	-	-	-	-
M. avenae	Lab	0	.95	100	100	100	100	-	-	-
A. pisum	Lab	0	0	.25	.60	-	-	-	-	-

FACTORS AFFECTING THE FLIGHT RESPONSES OF SELECTED PEST APHIDS
(HOMOPTERA: APHIDIDAE)

by

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The free fall technique was used to stimulate flight responses in selected aphid species. The aphids tested were cultured under greenhouse conditions, with temperatures ranging from 18-33°C.

The actual dropping of the aphids was done in a modified flight chamber with a dropping distance of 37.5 inches. A falling distance of 78 inches was used to test the validity of the technique. It was found that 37.5 inches is an adequate distance to stimulate flight.

By studying the individual flying life histories of S. graminum it was possible to conclude that variability among individuals within an aphid species could account for the measured variability in the results from the free fall technique.

Tests on the effect of temperature on aphid flight responses indicates that an aphid has optimal flight temperatures. A. fabae shows this optimal response between 20-30°C. and 35-40°C. S. graminum has its optimal flight responses from 20-40°C. Inhibition of the flight response was observed for A. fabae and S. graminum below 20°C.

The effect of light on aphid flight responses is quite evident. A. fabae has optimal flight responses at 2,000 foot candles and 200 foot candles. At 20 foot candles the response was moderate and below 2 foot candles, the response was low. S. graminum showed optimal flight responses at 2,000 foot candles, with a slight decrease in response at 200 foot candles. Below 20 foot candles the response was low.

Starvation had no effect on the initial flight responses of the aphids tested. The effect of starvation became evident in A. fabae and S. graminum at .5 day, beyond which the flight responses declined rapidly, terminating at 3.5 days with A. fabae and 1.5 days with S. graminum.

The flying lives of the aphids tested varied at the species level and at the infrasubspecific level in the case of R. maidis. The length of the flying lives varied between less than a day for A. pisum to more than nine days for A. fabae.

All the aphids tested were capable of reproduction before cessation of the flight response. The aphids varied in their ability to reproduce. The relationship between length of flying life and reproduction appears to be species specific. In the case of the biotypes of the corn leaf aphid (R. maidis), the most responsive biotypes possess the greatest reproductive capacity, while in S. graminum a comparatively poor flier, the reproductive ability reaches 100% by the second day of flying life.