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## Dispersion of the Host Specific Phytophagous Insects of Dunccecap Larkspur (*Delphinium occidentale*) in the Wasatch Mountains of Utah

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DISPERSION OF THE HOST SPECIFIC PHYTOPHAGOUS  
INSECTS OF DUNCECAP LARKSPUR  
(DELPHINIUM OCCIDENTALE)  
IN THE WASATCH MOUNTAINS  
OF UTAH

by

Robert L. Bayn, Jr.

A thesis submitted in partial fulfillment  
of the requirements for the degree

of

MASTER OF SCIENCE

in

Biology (Ecology)

Approved:

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Major Professor

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Committee Member

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\_\_\_\_\_  
Dean of Graduate Studies

UTAH STATE UNIVERSITY  
Logan, Utah

1975

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Robert L. Bayn, Jr.



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## ABSTRACT

Dispersion of the Host Specific Phytophagous  
Insects of Duncesap Larkspur  
(Delphinium occidentale)  
In the Wasatch Mountains  
Of Utah

by

Robert L. Bayn, Jr., Master of Science

Utah State University, 1975

Major Professor: Dr. Ivan G. Palmblad  
Department: Biology

Populations of Delphinium occidentale (Ranunculaceae) were monitored over two summers for the presence and dispersion of various life stages of several host specific phytophagous insects. Observations were made at several sites in the Wasatch National Forest east of Logan, Utah.

Two species of larkspur aphid (Aphis rociadae and Kakimia wahinkae) were encountered. Although dispersal of alate individuals resulted in widespread infestation of the host plant population, aphids occurred initially on the same one or few plants at each site both springs. Little coexistence of the two species of aphid on the same plant was observed, perhaps because they partitioned the host plant resource according to light intensity under the incomplete aspen canopy.



Several species of lepidopteran larvae, of uncertain host specificity, were observed. Two species (Autographa californica and Pyrrhia expremins: Noctuidae) are known from cultivated host plants. Eggs of an unidentified geometrid (Lepidoptera) were located on the host plants in large numbers and their dispersion was analysed. The eggs were distributed nonrandomly over the host plant population, but attempts to further characterize the pattern were fruitless. Parasitism of the eggs by an unidentified hymenopteran was observed.

Mortality of all larvae was high. Successful migration of larvae was not observed. Mature larvae were not sufficiently abundant to permit statistical study of pattern.

Mature fruits were examined at the end of the growing season for larkspur maggots (Hylemya laxifrons). Maggots were found in 85 percent of the inflorescences sampled. Pteromalids (Hymenoptera) were also found in an apparently parasitic relationship with the maggots in the fruits. Maggots were not found in the surviving fruits of inflorescences infested with either species of aphid.

Suggestions are given for future work.

## INTRODUCTION AND REVIEW OF THE LITERATURE

### Duncecap Larkspur as an Insect Host

Duncecap larkspur, Delphinium occidentale S. Wats. (Ranunculaceae) is a conspicuous component of the understory of aspen communities at 1830 to 3050 meters in the Western Rocky Mountains. Autecological characteristics of the plant have recently been studied by Holman (1973) while biotic interactions have been investigated by Fitz (1972). Other studies on the biochemistry and environmental requirements of D. occidentale have been conducted as it is among the poisonous range plants that may inflict losses on grazing livestock (Williams and Cronin, 1963, 1966, 1968).

Fitz's study revealed several groups of insects which feed largely or exclusively on D. occidentale. These insects included two species of aphids, several Noctuid larvae, a Geometrid larva, and a fly maggot. These insects direct their attack at the inflorescence of the host plant.

Delphinium occidentale is a long lived herbaceous perennial. The frost-resistant young shoots are among the earliest emergents of the understory and at that time are easily located. The unbranched stalks become the tallest herbaceous component of the understory.



Only Amelanchier alnifolia Nutt. and Lonicera utahensis S. Wats. of the woody component are consistently taller. As a result the inflorescences of the plant are generally well exposed to passing insects in flight and visual and contact stimuli as well as olfactory stimuli may aid insects in locating the plant.

The goal of the research reported herein is to: (1) determine some aspects of the dispersion of the above mentioned insects throughout several populations of the host plant, and (2) describe the partitioning of the host resource by the insects. Factors considered include: (1) conditions causing the insect to seek a new host plant (crowding, oviposition), (2) recognition of the host (color, odor), (3) conditions for acceptance of the host plant (growth stage, health, presence of other insects), (4) environmental conditions affecting the insect in the selection of an acceptable host (wind, light intensity, surrounding vegetation).

#### The Problem of Pattern

Most studies of phytophagous insect dispersion have been done on species infesting plants of economic value--crops in monoculture or landscaping cultivars. Aphids have been examined on beans (Banks, 1954; Taylor, 1962), potatoes (Bradley, 1952), corn (Cutright and Huber, 1928), limes (Dixon, 1971), peas (Fluke, 1929; Forsythe and Grisco, 1963), cabbage (McLaren and Pottinger,

1969), brussels sprouts (Pollard, 1969), crucifers (Root and Skelsey, 1969; VanEmden, 1969), sycamore (Dixon, 1969), and spruce (Parry, 1973). In such cases the uniform distribution of the host greatly simplifies the examination and interpretation of the insect distributions.

Examination of the insect fauna of non-cultivated plants is done largely from a descriptive viewpoint (e.g., Goeden, 1971) or with emphasis upon the effects suffered by a plant when the insect is present (e.g., Fitz, 1972; Green 1972).

Interpreting the pattern of an insect population over the pattern of its host is an open field of research. There are few established descriptive techniques applicable. Observations and data collection necessary for a rigorous quantitative description are prohibitively time- and manpower-consuming. Even done, such a description may be of little value for comparison with other studies due to the variability of the substrate of the study (host plant dispersion) as well as that of the subject (insect dispersion).

As a result, this study is largely qualitative in terms of conclusions although it represents many hours of examining, counting, and mapping of plants and insects in the field. It is hoped that this study may provide the framework for the design of further research into the spatial interactions of individual



insect taxa with the host plant.

### The Insects Considered

Fitz (1972) reported two host specific aphids, the russet colored larkspur aphid (Aphis rociadae Cockerell) and the green bronze larkspur aphid [Kakimia wahinkae (Hottes)] on D. occidentale at most of his study sites, with outbreak conditions at one site resulting in infestation of every flowering individual. The biology of the Aphides (Kennedy & Stroyan, 1959) and their flight behavior (Kring, 1972) have been extensively reviewed. These works indicate that the family includes members with many different strategies for survival which are reflected in their pattern of colonizing and using the host resource. The species considered in this work are known to prefer the inflorescence to the vegetative parts of its host and apparently overwinter in the egg stage (Fitz, 1972).

The lepidopterans considered are known to be polyphagous but the acceptable hosts, where known, do not include a large component of the plant species present in the habitat of D. occidentale. The alfalfa semi-looper [Autographa californica (Speyer) : Noctuidae] is reported to feed on Sambucus, Rumex, Malva species and some crucifers in addition to alfalfa and other legumes (Hyslop, 1912). Pyrrhia sp., another noctuid, is reported feeding on Polygonum, Juglans, Populus,



Salix, Rosa, Prunus, Betula, and Delphinium species (Forbes, 1954) and ovipositing on Geranium, Phlox, Chrysanthemum, and Ranunculus species in a lab study by Hardwick (1970). The three remaining lepidopterans reported by Fitz (1972) remain unidentified and their host specificity unknown.

Larkspur maggots (Hylemya laxifrons Hockett) are members of a large genus whose members have a high tendency towards monophagy although conclusive data for this species are not available. The larvae develop within the spur of the flower, then enter the fruit where they consume some or all of the seeds in one follicle prior to pupation (Fitz, 1972).

Initial investigations of the host plant revealed other insects which were common especially during the beginning of the growing season. These included thrips (Thysanoptera), stiltbugs (Neididae; Hemiptera), and plantbugs (Miridae; Hemiptera).

The first two groups became very abundant on some host plants when the stalks were elongating and succulent. Occasional necrosis and deformation of young stalks may be attributable to thrips. Stiltbugs with distended green abdomens were observed on the young host plants. Actual feeding was not observed.

Plant bugs were present in small numbers over most of the growing season. Feeding was not observed and no damage could be attributed to them. Although

not identified, it was determined that these were not larkspur mirid bugs (Hoplomachus affiguratus) studied elsewhere by Fitz (1972).

Two major factors precluded the addition of these insects to the study: (1) lack of host specificity in the study area and (2) lack of specificity of attack against the reproductive structures of the host plant.



## METHODS OF PROCEDURE

### The Study Areas

The populations of D. occidentale under investigation are among those used for previous work by Fitz (1972) and Holman (1973) in the Cache National Forest, Logan Canyon area, Utah. During the summer of 1973, populations were regularly examined near Pine Spring in Cowley Canyon (T12N, R3E, Sec. 32; elev. 2010 m.), near Tony Grove Lake (T13N, R3E, Sec. 3; elev. 2280 m.) and near Steep Hollow (T14N, R3E, Sec. 10; elev. 2250 m.). In 1974 study was intensified and restricted to the Pine Spring site. (Figure 1)

At all these sites the D. occidentale populations are under aspen (Populus tremuloides Michx.). At Pine Spring the understory also includes rudbeckia (Rudbeckia occidentalis Nutt.), senecio (Senecio serra Hook), serviceberry (Amelanchier alnifolia Nutt.), and American vetch (Vicia americana Muhl.) as conspicuous components. At Tony Grove the aspen canopy is incomplete as it nears stands of Douglas fir [Pseudotsuga menziesii (Mirb.) Franco]. Rudbeckia is very abundant; the other taxa mentioned above are rare and replaced by elder (Sambucus coerulea Ref.). The Steep Hollow site included bluebells [Mertensia ciliata (James) G. Don] as the

## LOGAN CANYON AREA

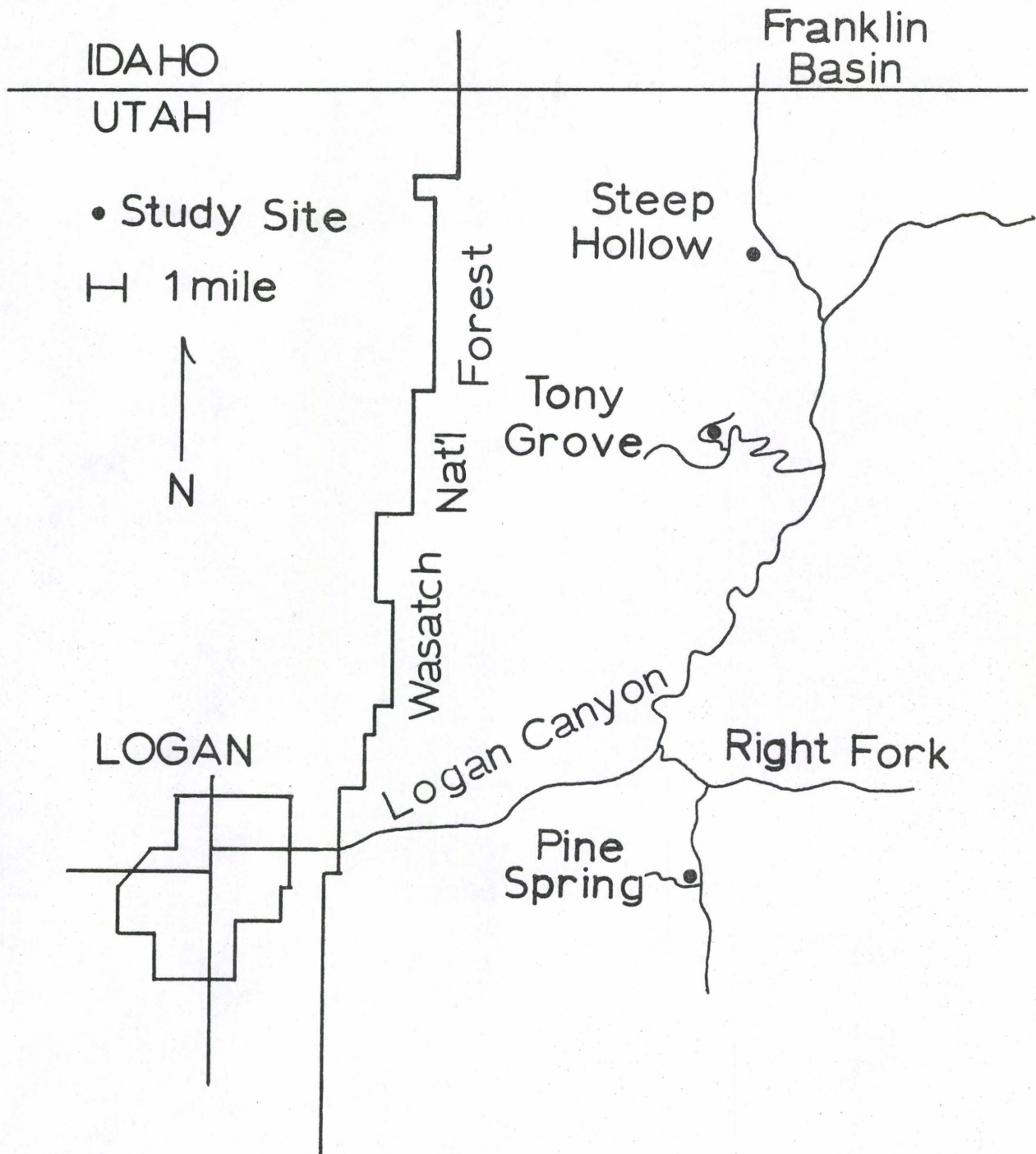


Figure 1. Logan Canyon Area (after Fitz, 1972)



most conspicuous understory component.

### Plots and Isolates

In 1973 a total of twelve, six meter square plots were established throughout the three populations. (Figures 2, 3 & 4) Locations were selected to give a sample of high and low plant densities under different amounts of canopy cover. All mature host plants were marked and mapped in each plot and individually inspected for insects on subsequent visits. Plants adjacent to the plots were also monitored and the rest of the population received cursory examination for aphid colonies and major damage from larvae. In addition to the plots, two isolated plants and two small clusters of less than ten plants were located along the road to the Pine Spring site and examined periodically.

In 1974 the observations in the Pine Spring site were expanded. A new plot of 100 meters by 100 meters was established to include the previous 6 by 6 plots. (Figure 2) Individuals were not precisely mapped in the new plot but were tagged and located within marked cells of 20 meters square. A thorough search of the area revealed the full extent of the host plant population and its isolation from other sources of insect dispersion.



## PINE SPRING STUDY AREA

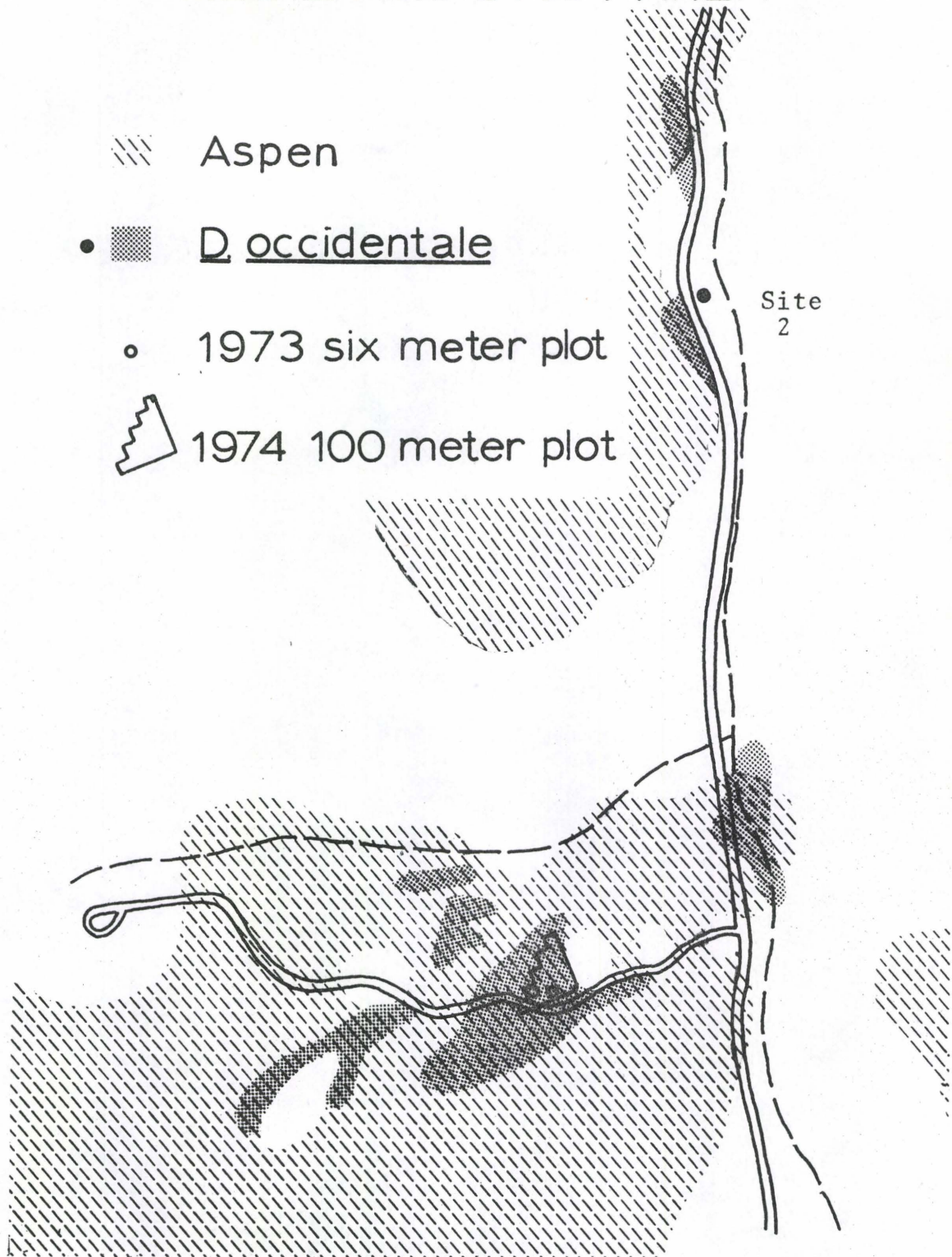


Figure 2. Pine Spring Study Area



## TONY GROVE AREA

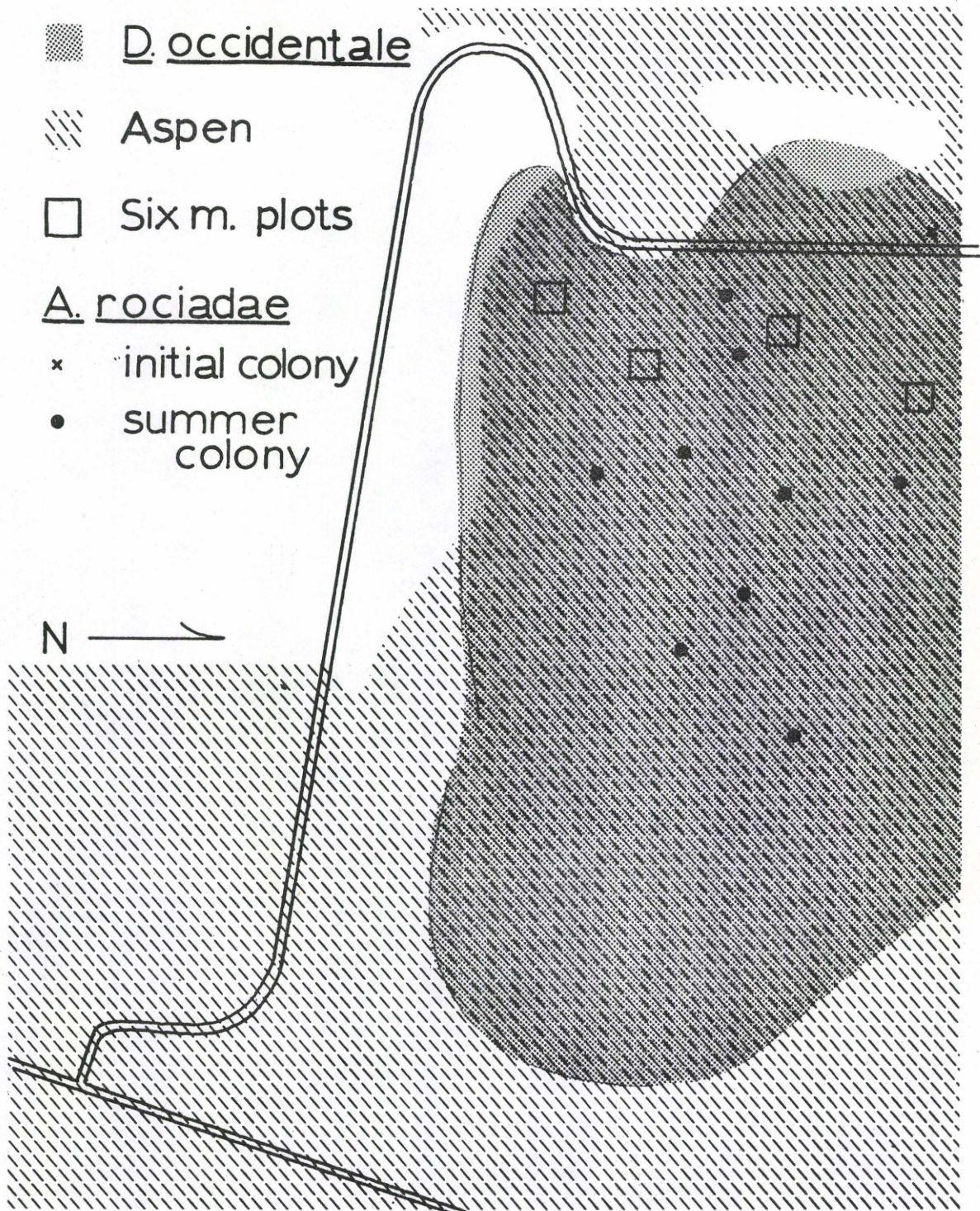


Figure 3. Tony Grove Study Area



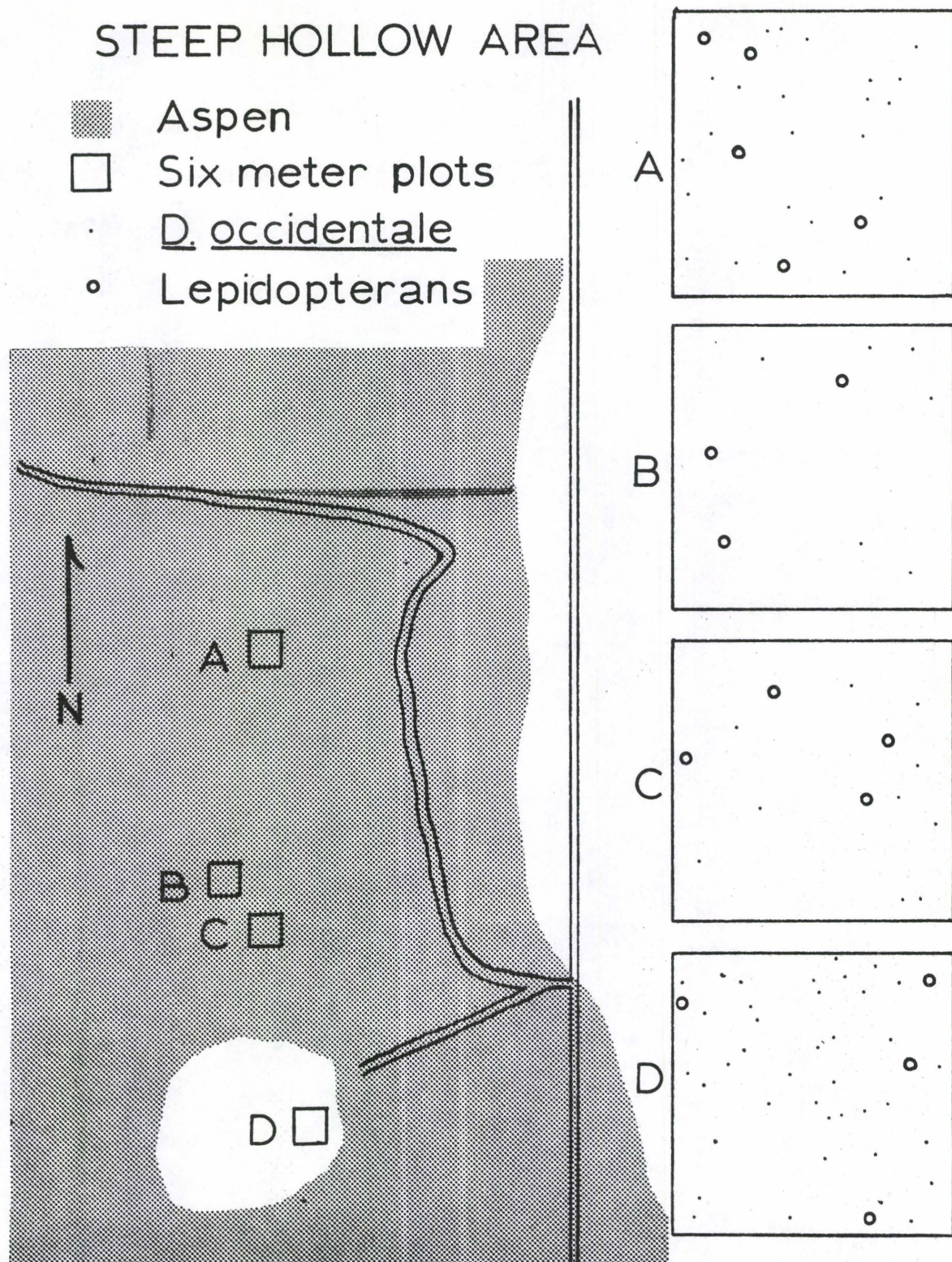


Figure 4. Steep Hollow Study Area. (presence data of 7/16/73)



### Examination Schedule and Methods

The sites were first visited in the spring just prior to completion of snowmelt in the area where D. occidentale shoots were just beginning to emerge. This occurred in mid-May at Pine Spring and mid-June at the other sites. Locating and mapping plants began then; the insects under study began appearing a few weeks later as the inflorescence buds developed. (Figure 5)

The Pine Spring site was examined about every four days; the other sites, every eight days. Visits continued into September when the plants were dry.

Each plant was examined in the following manner. The inflorescence was approached and examined without touching or disturbing it. This improved the chance of observing feeding insects or flying insects (especially parasites). A sheet of paper was then placed under the inflorescence to improve visibility and to retain insects that dropped off when the plant was touched. The stem was grasped and the inflorescence was rotated slightly for close examination. All insects and their activities were noted, larvae measured and condition and development of the plant recorded. In 1974 records were kept only for the insects under consideration and any new observations.

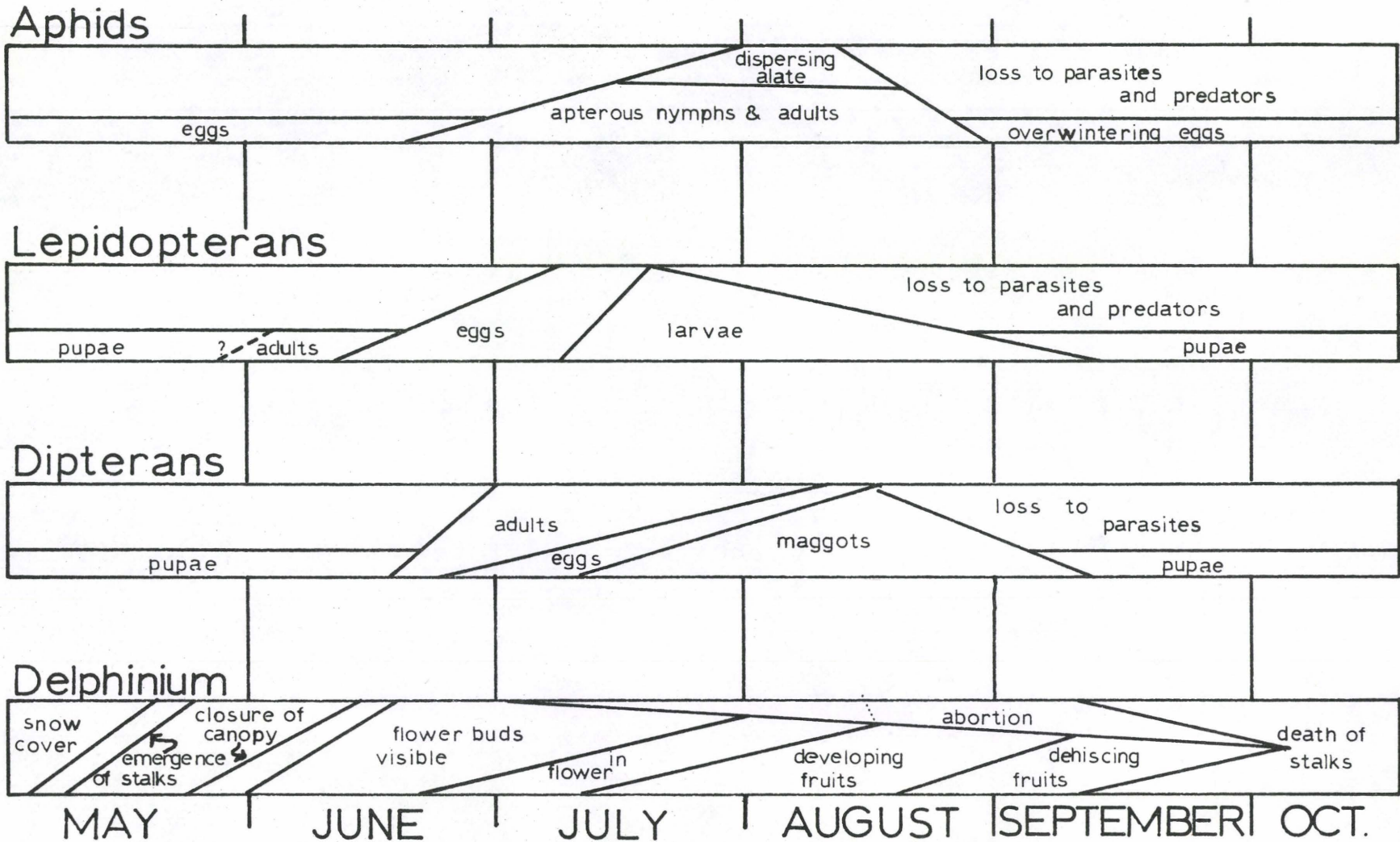


Figure 5. Development of host plants and occurrence of insect life stages at Pine Spring Study Area



### Inflorescence Enclosures

Some inflorescences were enclosed to protect selected insects on the plant. This was done for two purposes: (1) to protect the insect from predators and parasites so that mature specimens would be available for identification and preservation and (2) to assess the effect of the insect or colony alone on the host plant. The enclosures were designed to contain only the inflorescence on the erect plant in situ with a minimum of material, heat buildup, and effect on the surrounding vegetation.

The enclosures were constructed of wire and nylon stocking material. The wire was cut in 1.5 to 2.0 meter lengths and wound around a cardboard tube about 5 cm. in diameter creating a coil spring. A heavier spring steel wire was fastened to the flowering stalk with coated wire ties so the top of the wire was even with the top of the stalk. The coil spring was attached to the top of the wire and stretched down over the inflorescence. A cylindrical section of nylon material was then stretched over the coil and tied shut with coated wire. (Figure 6) The stretched nylon allowed direct examination of the inflorescence and insects if a bright background was placed behind the enclosure. It also allowed adequate air flow to prevent objectionable heat load. (Green pers. comm.)



Figure 6. Host plant inflorescence and wire-nylon enclosure

### Overwintering Studies

On February 20, 1974 the Pine Spring site was examined. Locations of plants harboring aphid colonies the previous summer had been marked by plastic flags on poles. In an effort to determine the importance of time of snowmelt on the success of any overwintering stages at the base of the host plant, approximately three-fourths of the snow cover was removed or added to several of the marked plants. The snow was about one meter deep at the time. The changes were made in a two meter circle centered on the host plant. Snow was not entirely removed so that insulation would not be totally lost during the winter.

The resulting spring snow patterns were examined on May 4, 1974.

### Photographic Equipment

All photographs were taken with a Minolta SRT101 with 58 mm lens (f1.4). Closeups utilized a bellows at minimum magnification, field of view 4.5 cm. Kodachrome 25 or 65 color slide film was used with existing light.



## RESULTS AND DISCUSSION

AphidsColony development and dispersal

The russet-colored larkspur aphid. During this study, populations of larkspur aphids did not reach the levels reported by Fitz (1972) for the same sites in a previous year. The russet-colored larkspur aphid, Aphis rociadae, was more abundant than Kakimia wahinkae and was first observed on June 24 during both summers of study. Three colonies were located in or near one of the six meter plots at Pine Spring in 1973. The next summer the same three plants were among the four plants harboring A. rociadae on that date. The fourth plant was outside the six meter plots and not examined in 1973. (Figure 7)

A similar observation was made at the Tony Grove site. One D. occidentale between two of the study plots harbored a large population of A. rociadae in 1973. Returning to the area July 1, 1974, the same plant again was host to a small population of the aphid. No other aphids were observed in the area, even on plants which had received dispersing alate (winged) aphids the previous summer. (Figure 3)



## PINE SPRING 100 METER PLOT

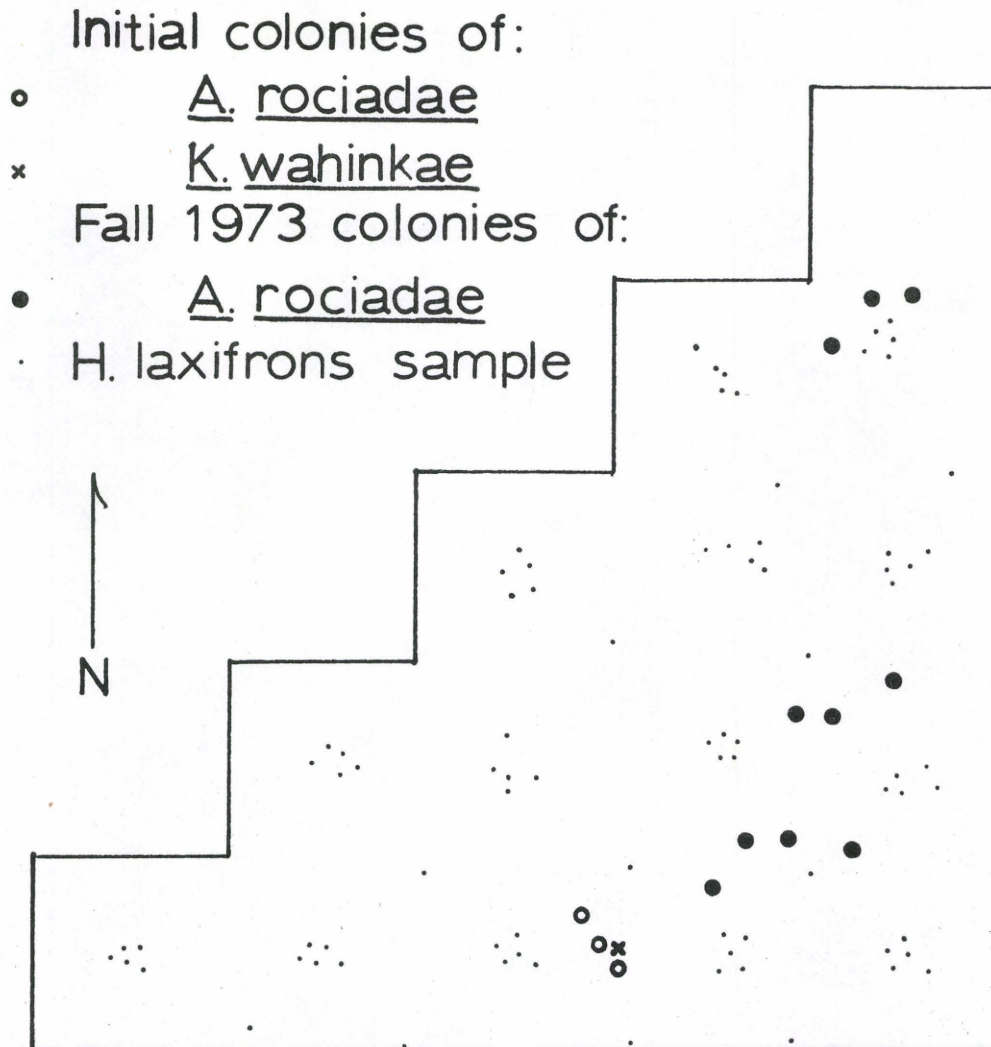


Figure 7. Pine Spring 100 meter plot showing location of aphids and of inflorescences sampled for larkspur maggots (Hylemya laxifrons)

In all of these cases there were additional host plants near the plant which harbored the initial populations of aphids each season.

Both years, these initial colonies became very large, covering the inflorescence and eventually the upper leaves of the host with a blanket of aphid nymphs and adults. Sticky collars of masking tape placed around the stalk at the base of the plant indicated that no migration or movements off the host were occurring by that route. Even adjacent flowering stalks of the same plant were uninhabited by aphids until late in the season (mid-August) when the host stalk began to show signs of deterioration under the heavy feeding.

In early July, alate, viviparous females were developing in established colonies and by mid-July they were located on other host plants in the area. (Figure 8) Kring (1972) reports that some species of aphids experience rapid atrophy of flight muscles after the dispersing alate accepts a new host plant and begins to produce a colony of nymphs. In other species, the capacity for flight is retained so that the alate may establish several colonies of nymphs on different host sites. It is unknown which type the larkspur aphids represent; however, the colonies of nymphs observed were always tightly grouped, never moved about on the plant and generally surrounded the winged mother of the colony. This suggests the possibility



Figure 8. Dispersing alate Aphis rociadae on a developing inflorescence of the host plant



that deterioration of flight muscles may have accompanied larviposition.

Numbers increased rapidly in these new colonies, just as in the initial colonies of the season. Development of a new generation of dispersing alate aphids from the newer colonies was never observed. All dispersing forms throughout the season appeared to develop from the initial colonies. New colonies were continually being established on additional host plants. The latest of these colonies did not develop large numbers before senescence of the host plant.

The dispersal of alate, as indicated by the establishment of new colonies, followed the general trend of spreading downhill at both Pine Spring and Tony Grove. A distinct fan-shaped pattern was evident from the single source colony at Tony Grove; however, the source colony was near the uphill boundary of the range of the host plant at that locality. (Figure 3) The several source colonies at Pine Spring obscured the pattern but they were centrally located in the host plant population and no new colonies were found uphill from the source. (Figure 7)

At the end of the 1973 growing season aphid-infested plants were marked for winter studies and for examination the following summer.

The green-bronze larkspur aphid. Kakimia wahinkae occurred with much lower frequency than A. rociadae. Established colonies were not found at the Tony Grove or Steep Hollow sites although a few individuals were observed during the growing season. A single colony was located in a six meter plot at Pine Spring the last week of June 1973. (Table 1 & Figure 9) It did not appear to increase as fast as nearby colonies of A. rociadae nor were additional colonies of the green aphid observed on the same plant. At the same time seven other colonies were observed at Pine Spring; the nearest about 45 meters uphill and outside the 100 meter mapping area. These colonies were all under more complete aspen canopies than were A. rociadae colonies. The darker green aphid may develop a prohibitive heat load in light levels tolerated by the lighter russet aphid.

Dispersal and establishment of new green colonies was observed in 1974. (Figure 10) The previously mentioned characteristics of lower density and slower population growth were apparent in these new colonies as well. The large number of initial colonies which were present throughout the host plant population made analysis of dispersing pattern impossible. Various means of tagging the aphids of a selected colony were considered and rejected (see Pettersson, 1968).



Table 1. Occurrence of aphids during 1973 in Pine Spring six meter plots and of larkspur maggots at end of season. See Figure 9 for plant locations.

Plot	Plant	Aphids											Maggots	
		June		July					August					Sept.
		26	30	5	11	16	25	30	3	8	13	17	31	12
1	1 <sup>a</sup>		1	12	30	120	150	250	200	200	110	100		0 <sup>c</sup>
	2					1	15	15	4					4
	3							25	25					3
	4													17
	5 <sup>a</sup>	1	6	25	50	150	200	275	250	200	180	100		0
	6 <sup>a</sup>					4	10	10	20	10				0
	7													1
	9								3					0
	11					12	50	130	150	180	200	120		0
	12								3	12	35	25		0
	18					1								0
2	21	10	25	70	100	120	200	250	300	400	650	200	100	0
	1 <sup>b</sup>													8
	3 <sup>b</sup>									50	100	250	20	6
	4													10
	5													2
	6										1	30		0
	8													1
	15										1			1

<sup>a</sup>Kakimia colony, all others Aphis

<sup>b</sup>A small raceme bearing 50 Aphis was transferred from #21 to #3 on 8/8/73.

<sup>c</sup>Mature, drying fruits were examined on 9/12/73 for larkspur maggots.



PINE SPRING SIX METER PLOTS  
 numbered D. occidentale

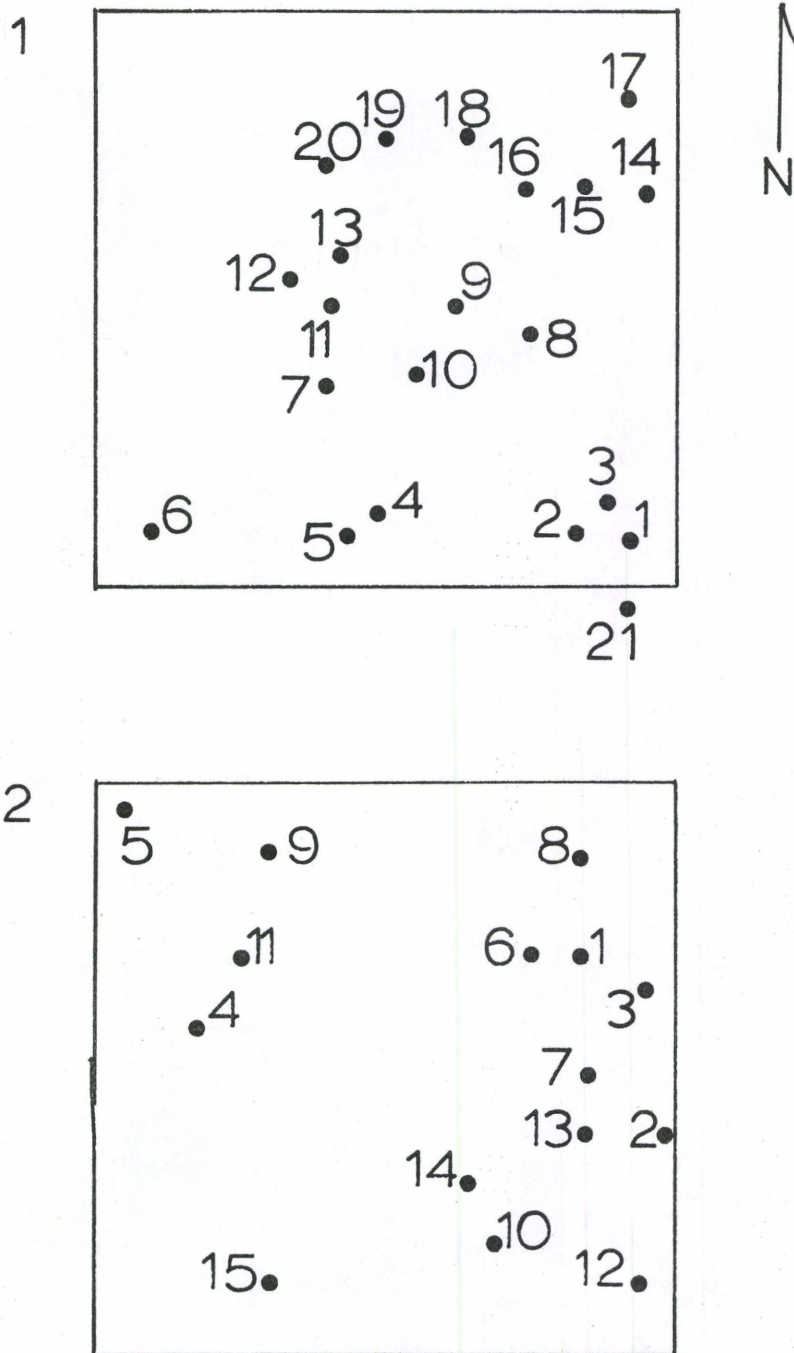


Figure 9. Pine Spring six meter plots showing location and number of labeled host plants (see Tables 1 & 2)



Figure 10. Dispersing alate Kakimia wahinkae on a developing inflorescence of the host plant



Other workers have suggested that some dispersing aphids are not attracted to potential host plants which already harbor other phytophagous insects (Root and Skelsey, 1969). During the peak of dispersal in August, 1974, fourteen host plants had small mixed populations of both A. rociadae and K. wahinkae on an inflorescence. (Figure 11) The russet aphid always outnumbered the green aphid either because the former arrived first or possibly because of the previously observed difference in rates of population growth. Apterous nymphs of both species were present indicating that the dispersing alate of each species accepted the host plant. The selection of the inflorescence by both species was apparently nearly simultaneous as neither species was observed alone on such plants during previous examinations.

This situation was observed late in the growing season and numbers of neither species increased to exclude the other before senescence of the plant. Alate aphids of one species were never observed in previously established colonies of the other species.

The occurrence of aphids on the same inflorescence with the other insects considered here was also rare. In only one case, at Pine Spring, was a small colony of A. rociadae established on a plant harboring a lepidopteran larva, Pyrrhia sp. Fall examination of the fruits of the four inflorescences which were host to the initial aphid colonies at Pine Spring revealed only one pupa.



Figure 11. A mixed colony of aphids on the maturing fruit of the host plant



of Hylemya laxifrons and one small pteromalid wasp.

#### Overwintering studies

The results of the overwintering studies were inconclusive due to the few host plants which were apparently overwintering sites for aphids. Only five plants of over five hundred in the study area at Pine Spring are known to have hosted aphids both years. Of them, four contained the initial colonies mentioned above and one received dispersing alate during the growing season, a different species each year. One of the group of four was selected for increased snow cover in the trial but no other plants with modified snow cover showed overwintering aphids the next spring. The initial colony with added snow cover emerged and developed on the same schedule with neighboring colonies with unaltered snow cover. The variation in time of complete snow melt from the Pine Spring site was about ten to fourteen days. This is greater than the difference in the time of snow melt between plants which received increased snow cover and adjacent plants with decreased snow cover. Thus snow depth is apparently not as important as topography in determining time of snow melt in the various microsites of the study area.

## Lepidopterans

### Leaf Rollers

The unidentified Noctuid leaf roller (Fitz, 1972) was the first insect to produce noticeable damage to host plants at the beginning of the growing season. Eggs were not observed. Larvae developed in leaves rolled over the terminal bud of the young stalk in mid-June. The bud was consumed and seed production for that stalk eliminated. Only five infested plants were observed in 1974. None were near the study plots of 1973. Attempts to enclose such stalks and rear the larva to adulthood were thwarted by unknown parasites.

### Occurrence of other larvae

Eggs were observed on bracts of the inflorescence of host plants from the third week in June through the first week in July both years. Oviposition by the female moth was not observed. The eggs were laid in irregular clusters of one to twenty-five (mean = 8) on about 15% of the plants examined at Pine Spring in 1974. (Figures 12 & 13) Approximately 2000 eggs were located. The oval, unornamented eggs were initially white, turning to a pale yellow-orange. The presence of clusters of both colors on one inflorescence indicated that ovipositing females did not avoid hosts already bearing eggs. These eggs were not similar to those described for Autographa californica by Hyslop (1912)

## PINE SPRING 100 METER PLOT

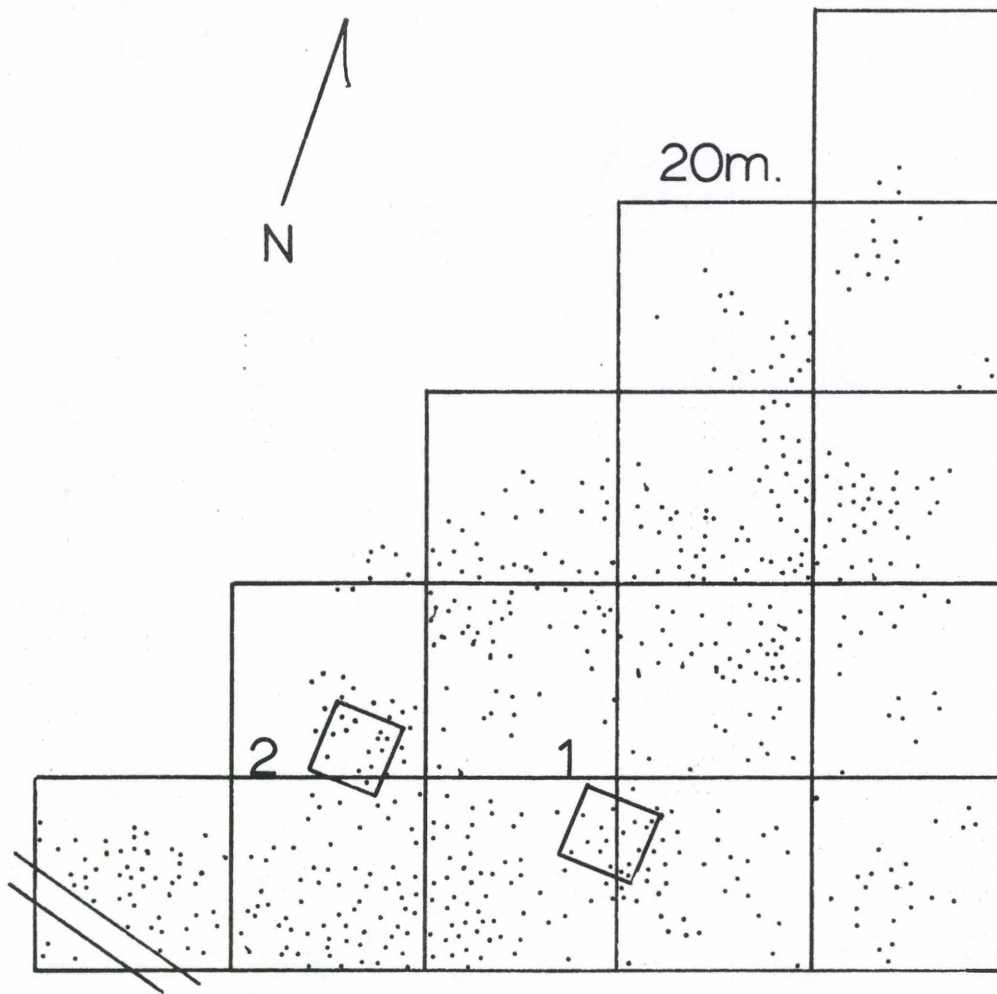
D. occidentale plants

Figure 12. Pine Spring 100 meter plot with location of host plants and six meter plots



## PINE SPRING 100 METER PLOT

Lepidopteran:

· eggs 6/20 27/74

◦ larvae 7/8/74

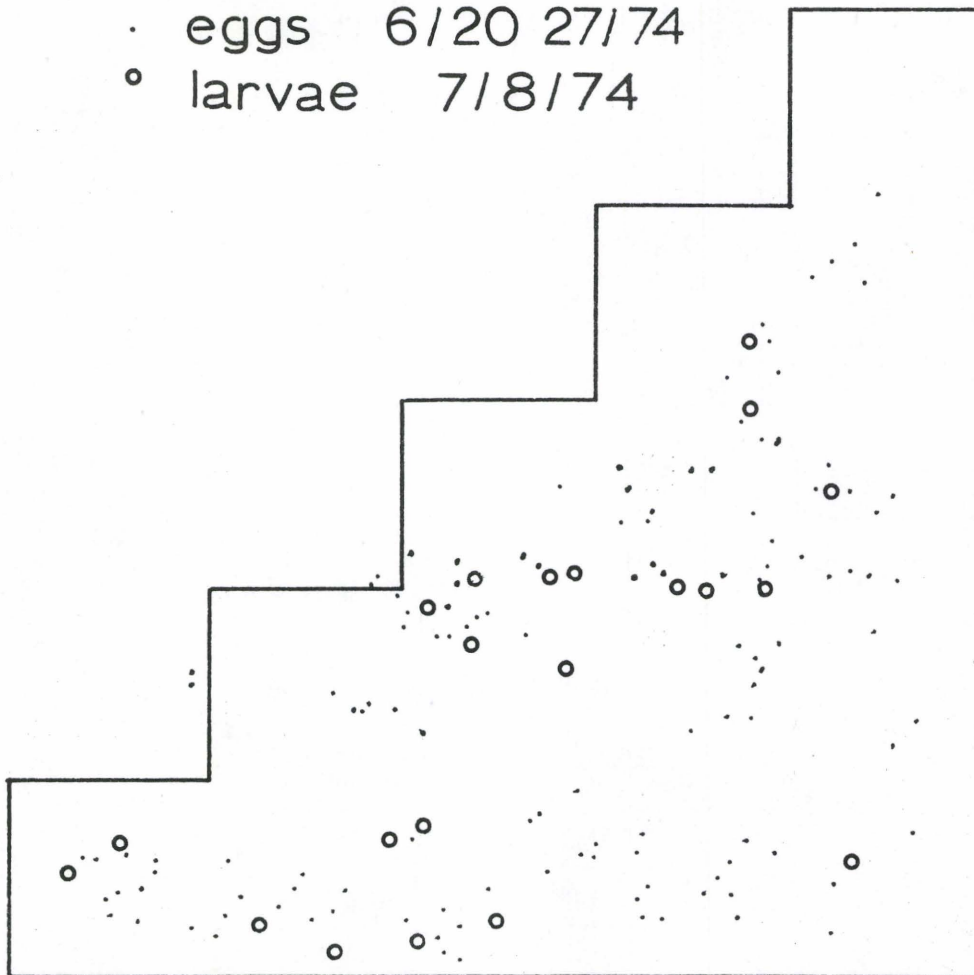


Figure 13. Pine Spring 100 meter plot with location of host plants bearing lepidopteran eggs and larvae during 1974

nor for Pyrrhia expremis by Hardwick (1970).

Various statistical tests have been applied to the distributional data (Figures 12 & 13) in an attempt to quantify the dispersion of the eggs.

A statistic to compare the distribution of eggs with the distribution of host plants was designed as follows. The maps of the Pine Spring Study Area were divided into 10 by 10 meter grids and the number of plants and plants with eggs (or larvae) was found for each grid. A frequency distribution for each count was made and the means determined.

$$[\mu_1(\text{plants}) = 8.93; \mu_2(\text{plants with eggs}) = 2.30]$$

The null hypothesis ( $H_0$ ) states that if the probability of oviposition on any plant were uniform then the distributions of the counts made in the grids should differ only by a measure of the difference in total density of plants versus plants with eggs. The scalar taken to represent this value is the ratio of the means of the two distributions ( $\mu_1/\mu_2 = 3.88$ ).

A  $\chi^2$  test comparison of the distribution of plants with eggs and the scalar reduced distribution of plants easily rejects  $H_0$  at a 95% confidence level ( $\chi^2(\text{df}=7) = 34.971$ ,  $\chi^2$  critical value = 14.0671). This result led to a number of tests attempting to extract factors of a pattern which would account for the nonrandom relationship.

The nearest neighbor relationship was investigated in greatest detail. The following data were taken from the map: distance from each plant with an egg to its nearest neighboring plant and to its nearest neighboring plant with an egg. This analysis was repeated while restricting the area considered for each plant with eggs to arcs of  $180^\circ$ ,  $120^\circ$ ,  $90^\circ$  and  $60^\circ$  from the subject plant and bisected by the line to its nearest neighbor with an egg.

Although oviposition was not observed it was hypothesized that behavioral traits of the female moth may have resulted in an identifiable relationship. Visual inspection of the map suggested the hypothesis that the female, leaving a plant after ovipositing, might be unreceptive to the stimulus of an otherwise suitable plant for a brief time after returning to flight. After this delay receptivity to stimuli of the host would be limited to those hosts within a certain distance of the flight path.

It was hoped that the distances measured in the various arcs would reveal a significant difference in means which would be most apparent in the arc which approximated the range over which a host was identifiable to the in-flight female. The nearest neighbor with an egg was selected as the most likely candidate as the next oviposition site (although this obviously could not have been true in every case).



In all categories of arc considered the mean distance to the nearest neighbor was less than the mean distance to the nearest neighbor with eggs but the variance in each sample was so great that in no case was the difference shown to be statistically significant. The values for the mean distance to the nearest plant with their 95% confidence limits are  $1.67 \pm 1.18$  ( $360^\circ$ ),  $1.86 \pm 1.41$  ( $180^\circ$ ),  $1.94 \pm 1.34$  ( $120^\circ$ ),  $1.98 \pm 1.51$  ( $90^\circ$ ), and  $2.01 \pm 1.34$  ( $60^\circ$ ) compared with  $2.43 \pm 2.24$  for the mean distance to the nearest plant with eggs.

Three eggs were observed hatching. The larvae were tentatively identified as geometrids. (Figure 14) The inflorescence was enclosed and the pupae collected in the fall to be reared to adulthood for identification.

Subsequent examination of the eggs revealed empty shells and no larvae present or no eggs nor larvae on slightly more than 90% of the host plants marked. (Figure 13) Three incidences of parasitism of these eggs were observed on June 20, 1974. A small wasp (under 2 mm) was observed ovipositing on (in) eggs on three different plants. (Figure 15) The wasp was not captured for identification.

Eggs of other species of lepidopterans were never observed although Autographa and Pyrrhia larvae were both more abundant in the study area than was the geometrid. The larvae of Autographa and Pyrrhia were first observed July 6, 1973 and July 1, 1974 at Pine Spring and



Figure 14. Geometrid larva on a developing fruit of the host plant



Figure 15. An unidentified hymenopteran ovipositing on a geometrid egg laid on an inflorescence bract of the host plant



July 11, 1973 at Tony Grove and Steep Hollow sites. Lepidopterans, primarily Autographa, were most abundant at the Steep Hollow site (Figure 4) with one larva per 9 square meters on July 16 compared to one larva per 15 square meters at Pine Spring. Up to five larvae, often representing more than one species, were observed feeding on single inflorescences. By the end of the growing season the numbers were reduced to occasionally two, more often one or no survivors per inflorescence.

There was considerable confusion in identifying early instar larvae. Hardwick (1970) described some variations observed between and within instars of Pyrrhia expremins, especially in coloration. (Figure 16) Additional variations were observed in this study. As a result, the data collected treats the lepidopterans as a group in early instars. Only a small portion of the larvae observed reached the final instar or the pupal stage where the species could be determined with some certainty in the field. (Table 2)

The variation in damage to the host inflorescence by a mature larva was notable. Among both enclosed and normal inflorescences individual larvae were observed to leave little evidence of chewing on the inflorescence or to completely strip the stalk of flowers and developing fruits. For enclosed stalks it was sometimes necessary to add an additional stalk from an adjacent host plant to insure sufficient food for development of the enclosed



Figure 16. Larva of *Pyrrhia expremis* on the calyx spur of the host plant

Table 2. Occurrence of lepidopteran eggs and larvae during 1973 in Pine Spring six meter plots. See Figure 9 for plant locations.

Plot	Plant	Eggs			Larvae						Identification of mature larvae			
		June			July			August						
		24	26	30	5	11	16	25	30	3		8	13	
1	2	9	9											
	3		9	9										
	4	2	2	5										
	5			4										
	7			18										
	8		4	4										
	9			5	5	2	3	1	1	1	1			( <u>Autographa</u> )
	10		10	10	10	2	5							
	11		1											
	12		3	3	3	1	2							
	14		11	11	8	5	3	1						
	16	6	6	9	9	1	1	1	1	1	1	1		( <u>Pyrrhia</u> )
	17		6	6	3	3	7	2	2	1				
	20	9	6	6	5	2	1	1						
2	1		3	5	5	2	2							
	4			1	1									
	5			3	10									
	8		3	9	6	1	3							
	9			1	1	1	1	1	1	1	1	1		( <u>Autographa</u> )
	10			1	3	2								
	11		2	2	2	2								
14			3	3	1	1	1							



larva. This variation in damage was observed to a small degree at the Pine Spring site as well as between sites during the 1973 studies. Seed destruction was much less among larvae-infested host plants at Pine Spring than at the other two sites.

Pine Spring is at a lower elevation than the other sites and host plants develop two and a half to three weeks earlier at the lower site. As was noted above, larvae were observed in 1973 only five days earlier at Pine Spring than at the higher sites. Breedlove and Ehrlich (1968) have reported that the relationship between flowering of lupines and oviposition by lycaenids can be correlated with the damage done to the host plant by the developing larvae. This suggests two possible explanations for the difference in damage to inflorescences of D. occidentale at the three sites. First, some winged gravid females may have been dispersed by some means to higher elevations where they laid eggs at the same time as their sisters of lower elevations and earlier than the local females. This explanation has implications for the gene pool of the populations involved. There are many known, unrelated examples of lepidopterans with a low tendency for dispersal (Ehrlich, 1961).

A second explanation is that different seasonal cues initiate the development of the host plant and the lepidopterans. The plants would be expected to

respond to a local or microenvironmental factor such as soil temperature, while emergence of the adult moth might be dependent on factors such as daylength which are uniform over a larger region.

#### Mortality factors

As the season progressed more host plants previously harboring larvae were observed without larvae. In most instances there was no evidence of what factor was responsible for the loss of the larvae. From isolated observations as well as the literature five different explanations, in two categories, are proposed to account for the loss of individuals.

First, there are two possibilities which result in larval losses from the host although leaving the host plant may not necessarily result in the death of the larva. Dethier (1959a & b) has studied migration in the larvae of a Nymphalid butterfly on Aster. He reported 80% larval mortality during migration and complete failure to locate a second host when the host plant was more than four feet away. Such migration attempts or the results of successful migration were never observed in the D. occidentale sites. An intermediate instar larva was never found on a host plant which had been previously recorded as uninfested by this insect group.



Although abandonment of the host plant was not observed, and not suspected to contribute to the success of the insects, accidental dislodgement may be an important contributor to loss of larvae from the host plant. This was observed while inspecting host inflorescences. When the stalk was touched, larvae would occasionally drop from the inflorescence onto the sheet of paper held beneath. These were mostly Autographa larvae. The geometrids occasionally dropped when they adopted their characteristic dead twig pose and their supporting prolegs chanced to be grasping a small bract or flower part which would not support their weight in that position. Once on the ground chances of the fallen larvae regaining a suitable host are probably no better than for larvae which normally migrate. It is suspected that disturbance of the plant by wind, rain or passing animals could have dislodged larvae.

The other category of loss includes those interactions which result directly in mortality and have no direct function in dispersal. Fitz (1972) cites predation of larvae by the paper wasp, Polistes fuscatus Hayward and a braconid wasp, Apanteles sp. Although Polistes was frequently observed rasping wood fibers from dead aspen boles in the study area, predation of, or interest in, the lepidopteran larvae was never observed. Predation by vertebrates was not observed and not considered likely in view of the feeding habits of those species



in the area.

Parasitism was observed on two occasions. A minute pteromalid wasp ovipositing on eggs has been mentioned above. One inflorescence enclosure containing a lepidopteran cocoon being reared for identification, yielded an ichneumon wasp about 12 mm in length instead of a moth.

One diseased Pyrrhia was observed on July 19, 1974. The rear half of the living larva was discolored and darkened. Its prolegs appeared functionless and all its movements slow. On the next visit to the site the larva was dead, completely discolored and clasping the stalk of the inflorescence.

#### Dipterans

Because there was little external evidence on the host plant of the presence of Hylemya laxifrons maggots in the flower spurs or developing follicles, progress of the maggot population was not followed throughout the growing season. The host inflorescences in the six meter study plots were examined for maggots or pupae in early September, 1973. At that time some fruits of each inflorescence were beginning to dehisce. Since dehiscence released the pupa from the follicle, seed damage was considered evidence for the presence of the maggot. In 1974, fully developed green fruits were collected on August 10 and 14, and stored in closed

kraft paper sacks until examination in early September when the fruits were dry.

Selection of samples was in a regular pattern. On August 10, thirteen inflorescences were collected. Using the intersections of the 20 meter grid, the nearest host inflorescence to each intersection was collected, if within five meters. Immediate examination of several inflorescences in the lab revealed the presence of maggots which pupated 24 to 48 hours after removal from the fruits.

Since six of the nineteen intersections in the study area had no host inflorescence within five meters of the intersection and many of the inflorescences had few developed fruits, a second sample taken on August 14, included parts of the inflorescence of the five plants closest to the center of each 20 meter grid. From each of the five inflorescences, the terminal raceme and one of the lowest lateral racemes bearing developed fruits were selected for the sample. This sample was intended to give representation to the full range of flowering times of host flowers of each inflorescence while restricting the bulk of the sample. These samples were processed in the same manner as the first.

In addition to sampling the plot area, several other inflorescences were collected for examination. The four inflorescences harboring the initial aphid populations were collected along with the inflorescences



of isolated plants located approximately 1000 meters away from the nearest population at Pine Spring.

The results of the sample in the study area are given in Figure 17. Of twenty-seven samples, twenty-three included one or more maggots or pupae of H. laxifrons. No explanation is apparent from the character of the host plant population or the study area, for the lack of maggots in four of the samples. Those plants may have been missed by ovipositors or some factor may have produced complete mortality of the maggots. Three of the negative results are in the sample of single inflorescences and only one in the pooled samples of five.

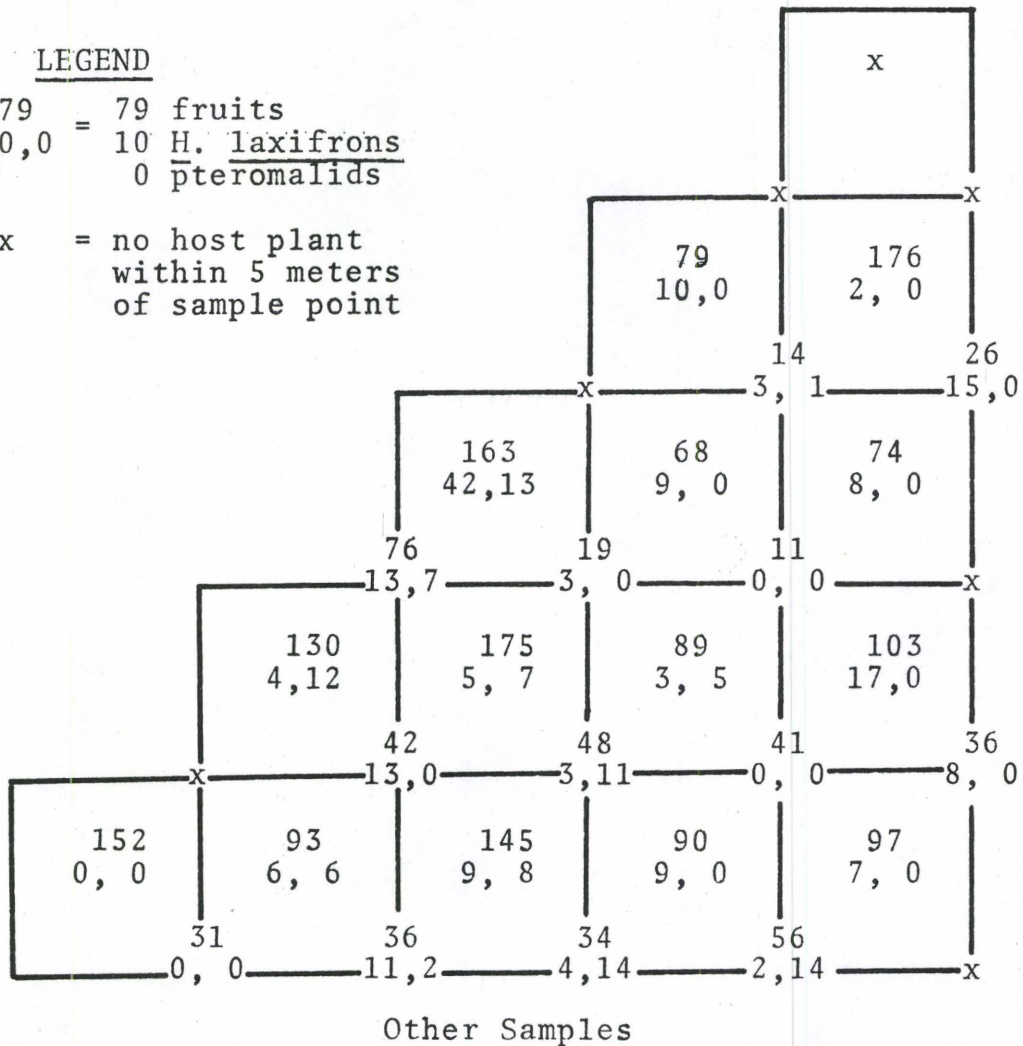
The isolated plants were infested with maggots comparable to the study plot sample, but the four plants which hosted aphids from late June, before the H. laxifrons oviposition season began (Fitz, 1972), were quite free of the maggots, only one being found in the entire sample.

An unexpected consequence of the processing procedure for sampling maggots was the appearance in the storage sacks of many small hymenopterans. Dissection of fruits revealed more, both in the adult and pupal stages, in cavities in the column of seeds of some follicles. These cavities appeared the same as those from which fly maggots and pupae were removed. (Figure 18) No trace of a maggot or pupa was ever found in a cavity



## PINE SPRING 100 METER PLOT

LEGEND  
 79 = 79 fruits  
 10,0 = 10 *H. laxifrons*  
       0 pteromalids  
 x = no host plant  
     within 5 meters  
     of sample point



Host plant sample	Inflorescences	Fruits	<i>Hylemya laxifrons</i>	Pteromalids
Aphid bearing plants	4		1	1
Site 2 population	7	191	35	10
Site 2 isolated plant	3	271	33	3

Figure 17. Data from inflorescences sampled for maggots and pteromalids, August 10 & 14, 1974 at Pine Spring Study area.



Figure 18. Seed column containing the pupa of Hylemya laxifrons removed from a dry follicle of the host plant. Pteromalids found in similar situations

occupied by the wasp. Although wasps were not found in samples without maggots or pupae (see Figure 17), a chi-square test of correlation barely fails to reject the hypothesis of independence at the 95% confidence level ( $\chi^2 = 3.76$ ,  $df = 1$ ). The hymenopteran has been identified as a member of the family Pteromalidae. Specimens have been sent to Dr. B. D. Burks at the Systematic Entomology Laboratory, U.S. National Museum, Washington, D.C. for specific identification. Most members of the family are parasites on invertebrates and many parasitize the pupae of dipterans (Muesebeck et al, 1951).

After this study was completed, reexamination of incidental insect specimens collected during the growing season revealed one pteromalid collected on July 1, 1974. The insect was hovering around a host inflorescence when captured. Oviposition was not observed.



## SUMMARY AND CONCLUSIONS

### Major Findings

The three groups of insects examined (i.e., aphids, lepidopterans and dipterans) exhibited different patterns of infestation of the host plant population. These differences appear to be the combined result of their distinct life cycles, dispersal capabilities and mortality factors, especially mortality attributed to parasites.

The dominant factor which influenced the pattern of aphid colonies was apparently the overwintering requirements of the eggs which gave rise to the initial colonies of the season. The dispersal of the alate aphids during the summer contributes little to the continued success of the aphids in the host plant population except to reintroduce the species to overwintering safe sites which become vacant.

Parasitism had little effect on aphid dispersion although literature shows that parasites are generally found during aphid studies (Hagen & van den Bosch, 1968). Parasites are not known to be responsible for the elimination of an aphid colony from a host plant. Parasites may slow colony development but they did not appear to alter the existing pattern of the aphids over the host plant population.

Pattern of lepidopteran larvae in the host plant population seemed to be influenced in just the opposite way. Overwintering success did not appear to restrict the dispersion pattern. Oviposition inoculated a large portion of possible host sites which were well distributed throughout the host population. Mortality factors work throughout the growing season to reduce the population and restrict successful larvae to safe site hosts which may vary from year to year.

In both of the above groups, the factors which control dispersion and population size of the insects may be important to the success of the host plant. Individual lepidopteran larvae or colonies of aphids can have a major impact on the seed production or vigor of the host plant. Control of the dispersion of these insects over possible hosts during the growing season restricted the effects of successful insects to a small portion of the population.

An entirely different relationship exists between factors which determined larkspur maggot dispersion and its effect on the host plant. Oviposition patterns resulted in a large portion of the host population being infested with maggots. Throughout the growing season the dispersion of maggots was little changed. Even parasitization by pteromalids did not reduce the impact of the maggots on the host plant population since such parasites do not kill their host until pupation,



which is after the destruction of seed in one follicle is completed. No factors have been identified which change maggot dispersion while controlling the H. laxifrons population.

#### Ideas for Further Investigation

This study has raised many questions, both central and peripheral to its objectives. Many questions deal with unknown factors in the life history of some of the insects considered. Although much is known about the families including these insects, only representative species which are also important to cultivated plants are well known.

One question, beyond the scope of this study, is apparent. Cottam (1954) described "prevernalization" of Aspen under which Delphinium occidentale occurs. Aspen is a relict species of a previous, more moderate climatic regime according to Cottam. At present, the stands reproduce only asexually by root suckers. As a result patches of the stand are genetically identical. Two genotypes exist in the area with respect to time of bud development and burst, and canopy closure in the spring, and senescence and abscission of leaves in the fall. The two genotypes on one site are evidenced in spring and fall by approximately ten day difference in leaf development schedule. In view of previous discussion of synchronization of development of insects



and host plant, these discrete alternatives of canopy closure and attendant microenvironmental factors (light, temperature and moisture) in the understory may affect insect presence, dispersion, or success on D. occidentale or other components of the understory.

### Aphids

Several questions have already been alluded to in previous discussion of the aphids on D. occidentale. It is presumed that the aphid eggs overwinter in very close proximity to the host plant. It is not known what additional constraints result in so few host plants harboring successfully overwintered eggs (Sutherland, 1968).

The two species of aphids did not exhibit extensive competition for hosts. Their dispersion was different and possibly the result of differing tolerances to microenvironmental conditions such as light intensity.

Impact of predators and parasites on A. rociadae and K. wahinkae remains unknown although procedures for such study are well established (Hodek, 1966; Knutson, 1973).

Time of degeneration of flight muscles of dispersing alate, as already mentioned, is not known (Kring, 1972).

Although some dispersing aphids apparently tend to avoid hosts which already harbor other feeding insects, this behavior is not confirmed nor is the mechanism

for this perception known (Root & Skelsey, 1969).

### Lepidopterans

A major question which still exists among the lepidopterans studied is that of identification. It is hoped that specimens collected as part of this work may be successfully reared and identified. Subsequent adult activity, including oviposition may then be observed in the field, improving the determination of egg presence on D. occidentale and the extent of use of other possible host plants. The attempt made at quantifying egg dispersion could be handled more effectively with observations of oviposition since that would reveal the sequence of plants visited by each female. Analysis of the data presented in this paper relied on a simple "rule" to define the next plant visited. The analysis also avoided the problem of distinguishing the eggs laid in the same area by different females. Resolution of these problems with oviposition observations could reduce the variance encountered in the data presented herein. Procedures for such work are suggested by Ehrlich and his students as well as others (Labine, 1968; Sharp, Parks, & Ehrlich, 1974; Stern & Smith, 1960).

More intensive observations of larvae could reveal actual mortality factors and their relative importance. Several parasites and predators have been observed during this and previous studies (Fitz, 1972) but their impact on the larval population has not been assessed.



Survival of larvae which left the host plant is also unknown.

The observations and suggestions made concerning varying impact of feeding lepidopteran larvae on the host plant seed production with altitude of the host plant population require more study. Study of oviposition times at different altitudes as well as a determination of the source of ovipositing females could reveal the mechanism of the observed effect that the larvae have an increased impact on reproduction of host plants with an increase in altitude.

### Dipterans

The primary question raised concerning the larkspur maggot is the role of the pteromalid. If indeed a parasite on the maggot, its numbers indicate an important effect on the subsequent fly population. Its life history and specificity as a parasite are unknown.

A life history of the larkspur maggot, especially adult stages, is not well defined. Additional mortality factors must be at work on the pupal and adult stages during winter and spring in view of the large number of pupae recovered in the sample taken in August.

It is hoped that this thesis can provide a general framework of information and expectations from which more detailed studies into these individual questions may be designed. Considerable time is devoted in such



studies gathering preliminary information to delimit questions and provide an approach to data collection. By examining many potential areas of work at the same site, the data collected may be useful in the preparation of more than one question for study. This study represents the large amount of time necessary in early stages of isolating questions. Its intended value is in preparing these questions for immediate work.

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