Overwintering, springtime development and migration of some Aphidae, including Myzus persicae, of northwestern Montana
by Daniel Frederick Aldrich

A thesis submitted in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE in Entomology
Montana State University

Abstract:

The green peach aphid, Myzus persicae(Sulzer), was found overwintering in northwestern Montana as eggs on peach, Prunus persicae L. The potato aphid, Macrosiphum euphorbiae Thomas, was found overwintering as eggs on wild rose, Genus Rosa. Other species of Aphidae overwintering in the area on Prunus domestica L., .P. americana Marsh., P. virginiana L., and on Crategus spp. are identified. Spring hatching of Aphidae within the area was initiated within the last two weeks of March in 1977 and continued until at least mid April. Hatching was not found co-incident with a mean monthly maximum temperature of 4°C, but it occurred immediately thereafter (5°-7°C). Hatching was prior to the phenological date of first leaf-budding on common purple lilac, Syringa spp.

The 1977 spring migrations of Aphidae in northwestern Montana began in the second and third weeks of May and peaked one month later in mid- and later-June. Migrations were initiated during the period of mid-bloom for common purple lilac. Aerial aphid catches were directionally significant ($p = 0.01$) and appeared to be related to prevailing winds.

The primary reservoir of potato leafroll virus within the area was believed to be infected potato and tomato plants in home gardens.

Potato leafroll virus and some of the pertinent biology of its primary vector, Myzus persicae, are reviewed.

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ABSTRACT

The green peach aphid, *Myzus persicae* (Sulzer), was found overwintering in northwestern Montana as eggs on peach, *Prunus persicae* L. The potato aphid, *Macrosiphum euphorbiae* Thomas, was found overwintering as eggs on wild rose, Genus Rosa. Other species of Aphidae overwintering in the area on *Prunus domestica* L., *P. americana* Marsh., *P. virginiana* L., and on *Crategus spp.* are identified. Spring hatching of Aphidae within the area was initiated within the last two weeks of March in 1977 and continued until at least mid April. Hatching was not found co-incident with a mean monthly maximum temperature of 4°C, but it occurred immediately thereafter (5°-7°C). Hatching was prior to the phenological date of first leaf-budding on common purple lilac, *Syringa spp.*

The 1977 spring migrations of Aphidae in northwestern Montana began in the second and third weeks of May and peaked one month later in mid- and later-June. Migrations were initiated during the period of mid-bloom for common purple lilac. Aerial aphid catches were directionally significant ($p = 0.01$) and appeared to be related to prevailing winds.

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Potato leafroll virus and some of the pertinent biology of its primary vector, *Myzus persicae*, are reviewed.

INTRODUCTION

Flathead and Lake Counties (Flathead Valley) have been under potato production for around 50 years. Since 1970, the yearly acreage planted to potatoes has been between 3000 and 3500 acres (1200-1400 ha) and has yielded an annual harvest-crop value of a little less than $10,000,000, or approximately $3000 per acre. This represents nearly 50% of the total statewide acreage under potato production and at least 30% of the combined revenue from potatoes, wheat and hay for these counties (Montana, 1977a).

Well over half of the potato acreage in the Flathead Valley is devoted to certified seed potato production. Certification of this seed requires persistent disease control. Potato leafroll virus (PLRV) is the least tolerable of all the virus diseases of seed potatoes. The highest grades of seed potatoes, Nuclear and Elite I and II, allow no incidence of this disease in stocks. Foundation and Elite III grades tolerate 0.3% or less PLRV disease, and all the Certified grades will allow only 1.0% incidence of PLRV (Montana, 1977b). Potato crops disqualified as seed are reduced in value 25% to 50%. In addition, severe leafroll can reduce tuber yields 92% over healthy plants (Harper et al., 1975).

Except for the spread of leafroll via the propagation of infected tubers, the sole known means of its spread is by aphid-vector transmission. Of about 10 known aphid vectors of PLRV, the green peach aphid, Myzus persicae (Sulzer), is the most efficient (Kennedy et al., 1962). Although PLRV has been incident within the Flathead Valley for several years, the presence of the green peach aphid was not verified until 1976.[1]

This study was undertaken to investigate the overwintering of the green peach aphid within the Flathead Valley and to determine the spring migration patterns of aphids, as a group, as these migrations related to the spread of virus diseases in potatoes. It was intended to identify potential factors affecting the prevalence and increase of this aphid and the incidence and spread of potato leafroll virus.

To approach a management plan for the control of Myzus persicae and the spread of potato leafroll virus, an understanding of the virus-vector relationship is necessary. A literature review of potato leafroll virus (Appendix D) and some of the pertinent biology of Myzus persicae (Appendix E) is included here to provide background understanding of the complexities of this relationship. The conditions that facilitate the outbreak of disease or trigger a virus-vector relationship favorable for disease spread are multiple and interrelated. While these reviews suggest many single factors important in approaching a management plan for virus-vector control, any one, or

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[1] O. G. Bain, 1976, Environmental Management Division, Montana State Dept. Agriculture, 1300 Cedar Ave., Helena, Montana 59601. Personal communication.

combination of them cannot be substituted for an in-depth understanding of the virus-vector interplay in a particular control circumstance. Therefore, the present work does not proffer a complete management plan, but rather identifies some of the factors particular to the Flathead Valley as these factors relate to the body of understanding included within the literature reviews.

DESCRIPTION OF THE STUDY AREA

The area investigated by this study, the south Flathead Valley, is located between 114° and 114°30' west longitude and between 47°20' and 48° north latitude. It comprises most of the area of Lake County, Montana and lies within the southern-most region of the Rocky Mountain Trench, a structural depression stretching through British Columbia, Canada, to about 160 km south of the study area on the west side of the continental divide. The valley is bounded by the Mission Mountains on the east, rising abruptly from the valley floor at about 900m up to around 2500m, above alpine terrain. On the west side of the study area is the Flathead River. Beyond the river the topography rises into more arid coniferous forest but less abruptly than east of the valley basin (Fig. 1).

The valley was made by geological uplifts and downdrops along fault lines. The valley depression was enhanced by glacial action that scoured the land surface and left numerous moist potholes (Owen, 1958). The Flathead River Basin abounds with more water than any other basin in Montana, and this water drains through the Flathead Valley (Fig. 2) (Montana, 1976).

The study area is around 988,000A (400,000 ha), one-tenth of which is water area. Over half the land surface of Lake County is montane forest, with another 30% equally divided between rangeland and irrigated pasture. Only 2% of the county is devoted to irrigated

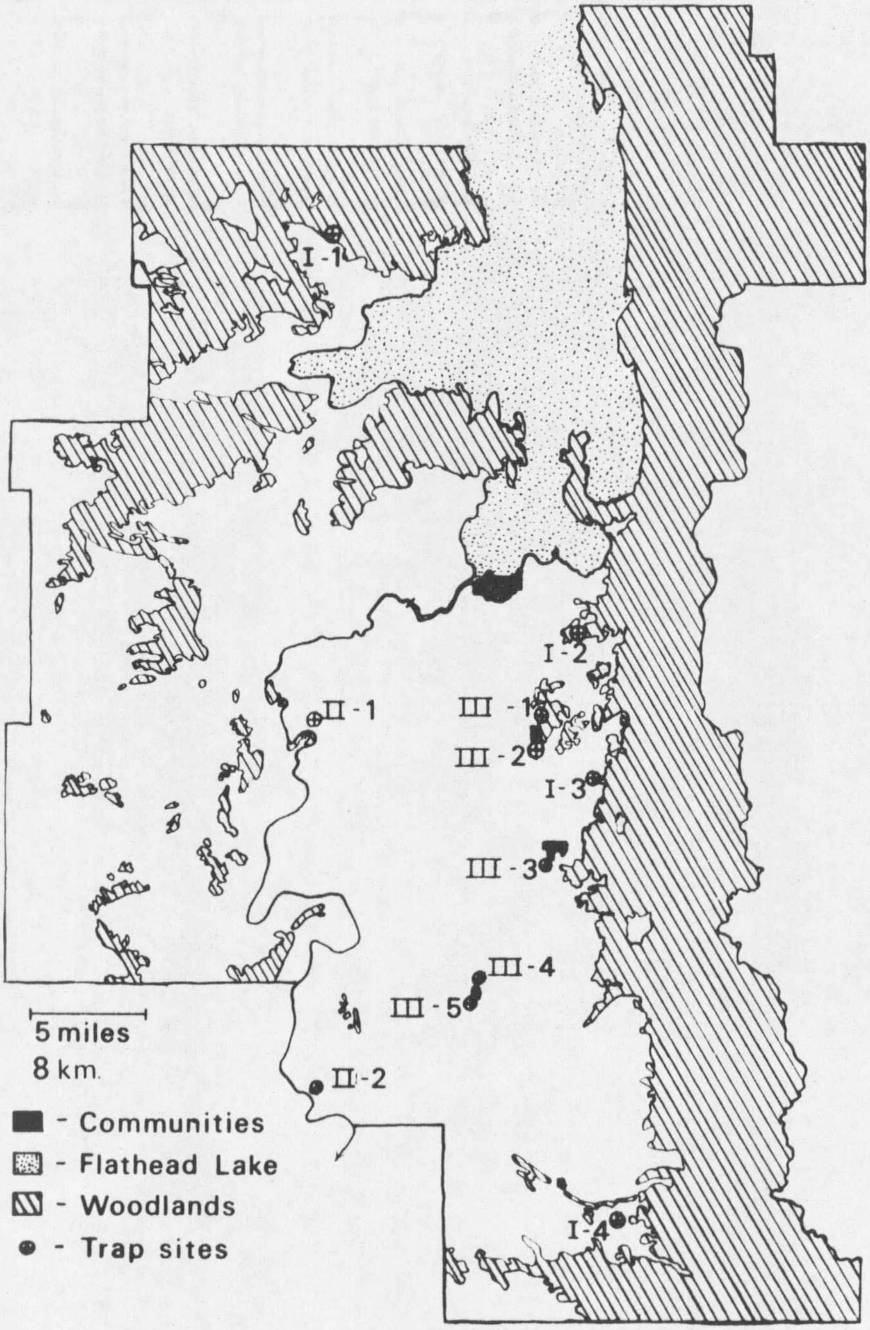

Figure 1. Aphid trapping sites in relation to suburban communities and montane woodlands in south Flathead Valley of northwestern Montana.

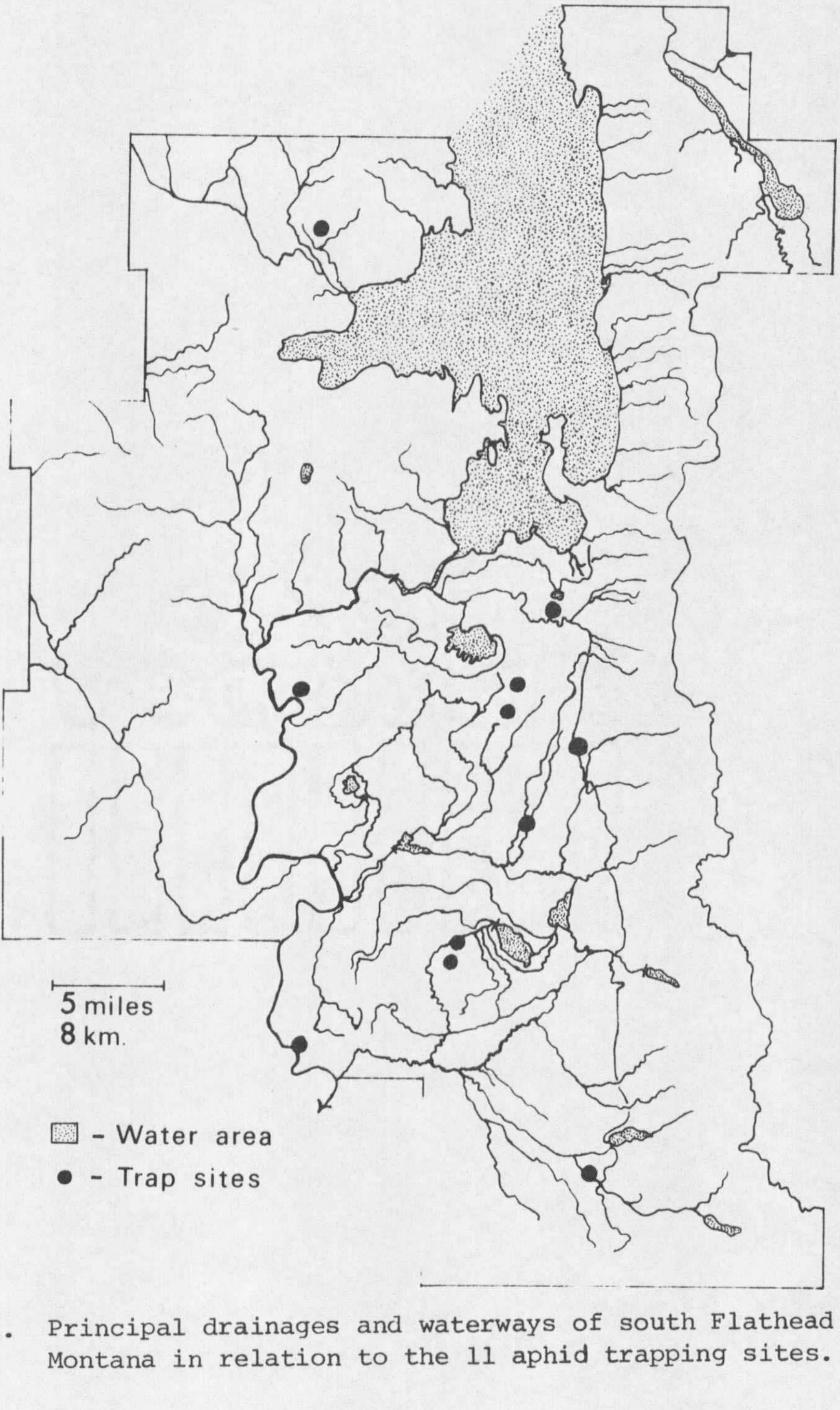

Figure 2. Principal drainages and waterways of south Flathead Valley, Montana in relation to the 11 aphid trapping sites.

cropland (1000-1200 ha potatoes). About one-tenth of 1% of the land area is in orchards. These are primarily confined to the immediate vicinity of Flathead Lake (Lake County, 1977). The lake moderates the microclimate of the adjacent area enabling cultivation of sweet cherries (Prunus cerasus L.). Other Prunus species (plum, apricot, peach) also are grown to a lesser extent around the lake and at scattered rural and urban homesites.

Lands of south Flathead Valley planted to wheat and other small grains have been declining in area for the past 25 years. There has been a shift from the cultivation of small grains to growing hay and pasture. About three-quarters of the barley and oats used in Lake County is imported from other parts of the state. Hay pastures are most widely planted to timothy (Phleum pratensis L.), clover (Trifolium repens L., T. pratensis L., T. hybridum L.) and alfalfa (Medicago sp.)(Lake County, 1972).

Most of the agriculture of the valley is livestock oriented. However, because non-agricultural demands are increasing land values more than profitable agricultural operations, there is a constant stress on agricultural land to maximize production. On rangelands, particularly on the more arid western side of the Valley, grazing pressure is changing the basin grasslands from rough fescue types (Festuca scabrella Torr.) to Idaho fescue (Festuca idahoensis Elmer), bluebunch wheatgrass (Agropyron spicatum (Pursh.) Scribn. & Smith) and cheatgrass brome (Bromus tectorum L.) types (Taylor et al., 1974; Mueggler and Handl, 1974).

Population densities of south Flathead Valley are currently about 10 persons per square mile (2.59 km^2). Forty-four percent of the population resides in suburban communities. Some present community populations shown in Figure 1 from north to south are Polson, 3600; Pablo, 325; Ronan, 1500; Charlo, 230; St. Ignatius, 925. The total population of Lake County is around 17,000 people. The rural agri-business population of the county has been declining for the past 30 years. Population growth projections suggest a stable growth due mainly to a limited influx of manufacturing industry. Farm and agriculture-oriented population is expected to continue declining in the future (Lake County, 1977).

The valley is frequented by a dry continental-type climate influenced by Pacific coastal and Arctic weather. Pacific maritime air predominates during winter, resulting in a milder climate than is characteristic of continental air masses elsewhere. The interaction of arctic air causes cool spells in the valley about half as often as east of the continental divide in Montana. In the immediate vicinity of Flathead Lake, the growing season is about 140 days. The study area, south of the lake, has a 100-120 day growing season. Fifteen to twenty inches of annual precipitation is characteristic of the valley, but considerably more than this accumulates in the surrounding mountains (Montana, 1976).

Frontal weather from Pacific coastal air moves across the valley from the west. Westerly and southwesterly winds dominate these fronts. Northern arctic air overflowing the continental divide enters the valley from the north and northeast.

MATERIALS AND METHODS

Flatblack sticky traps were located at 11 trapping sites toward the southern end of Flathead Valley. The traps were constructed from metal-rim-reinforced plastic cylinders measuring approximately 171 cm in circumference by 28 cm high (Fig. 3). Plastic sheets were wrapped around the cylinder and fixed to it with brass fasteners at three locations. A 10.7 cm (4 inch) wide strip in the center of these sheets was coated with Tack-trap R (polybutylene) to provide a circular trapping area 10.7 cm by 171 cm.

Each trap was placed atop a wooden post driven into the ground until the top edge of the trapping surface approximated 2 meters height. This height was selected as the average height normally found for the boundary layer (Rosenberg, 1974), and it approximated the location of the wind shear layer. The traps were painted flat black to have no attraction for aphids. The traps were intended to measure the aerial aphid density near the boundary layer.

Traps were oriented at least 5 meters away from any vegetation that approached their height to take maximum advantage of prevailing winds. Traps were also oriented to be minimally affected by winds incited by localized topographical and vegetational variations near the trap site.

Trap catches from the 11 sites were adjusted to 9-day trapping intervals for comparison. The first interval was chosen arbitrarily

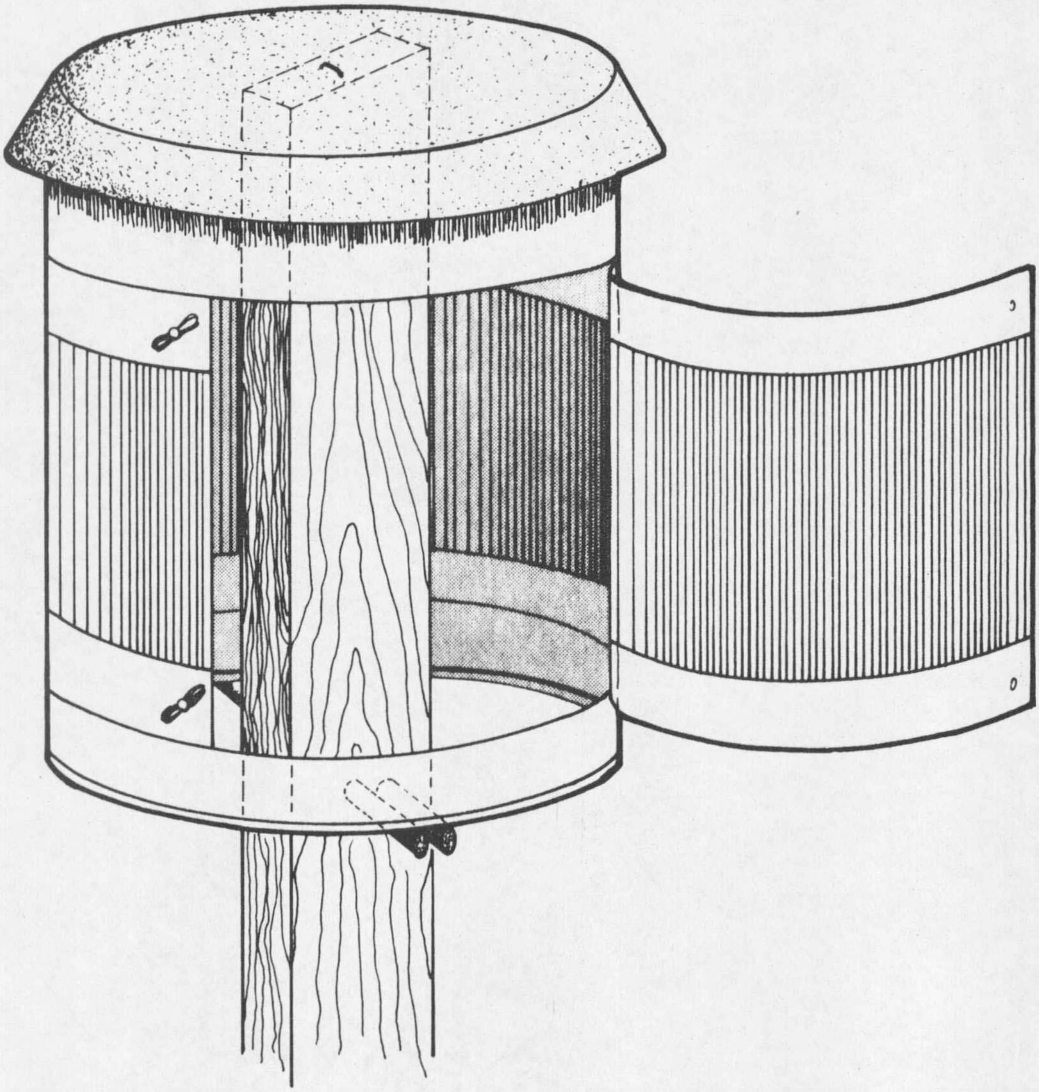

Figure 3. Black sticky trap used for aphid trapping in south Flathead Valley, Montana.

to correspond with the first alate aphid trapped. It began on May 16, 1977.

At several rural locations within the study area, chokecherry and hawthorn were monitored for spring emergence of aphids and colony development. Terminal twigs on these shrub stands were tagged and checked for aphid eggs and nymphs. Official maximum and minimum temperatures from Kalispell, north of Flathead Lake, Polson and St. Ignatius were analyzed for correlation, if any, to spring hatching dates, colony development and alate formation.

Sweep-net surveys of crop and pasture lands and inspections of home gardens were conducted to determine aphid distribution.

Phenological dates for purple common lilac, *Syringa sp.*, were recorded at the northern- and southern-most trap sites for possible correlation with aphid emergence.

Collections of developing and mature apterous and alate aphids were taken from *Prunus virginiana* L., *Prunus domestica* L., *Prunus americana* Marsh., *Prunus persicae* L., *Crategus spp.* and *Rosa spp.* for identification.

Description of Trapping Sites

Three general types of trapping sites were selected. Site I traps were placed adjacent to woodlots or forest cover (Fig. 1). These were at higher elevations than the other site-types. Ponderosa pine (*Pinus ponderosa* Dougl.) was the most conspicuous gymnosperm near these sites though larch (*Larix occidentalis* Nutt.), white pine (*Pinus monticolor* Dougl.), Engelmann spruce (*Picea engelmanni* (Parry) Engelm.) and a few species of fir (*Abies sp*. Mill., *Pseudotsuga spp*.) also occurred. Along moist slopes and drainages skirting the grassy areas where traps were located frequent shrub stands included *Crategus douglasii* Lindl. and *Crategus chrysophyta* Ashe (hawthorn), *Rosa spp*., *Amelanchier spp*. (service berry), *Sambucus coerulea* Raf. and *Sambucus melanocarpa* A. Gray (elderberry), *Symphoricarpos spp*. (snowberry or buckbrush), *Prunus americana* L. (wild plum), and *Prunus virginiana* L. (chokecherry). The most frequent grasses near Site I traps were *Agropyron repens* (L.) Beauv. (quackgrass) and *Poa spp*. (bluegrass). *Agropyron spicatum* (Pursh.) Scribn. and Smith (bluebunch wheatgrass) was less common.

Site II traps were located on range and grasslands adjacent to some cultivated lands. These sites were on the more arid western side of the study area and were at lower elevations than the other site-types. Though no woodlots were near to these sites, isolated cottonwoods (*Populus sp*.) and willows (*Salix sp*.) occurred near irrigated lands or in moist drainages within a kilometer in every direction from the sites. *Crategus chrysophyta* Ashe and *Crategus douglasii* Lindl., *Prunus virginiana* L., and *Prunus americana* L. also occurred along drainages and in moist undisturbed depressions. Figure 2 shows the relationship of all the trapping sites to the principal drainages and waterways of the study area. *Purshia tridentata* (Pursh.) DC. (bitterbrush), *Artemisia frigida* Willd. (fringe sagewort) and *Artemisia tridentata* Nutt. (big sagebrush) were also found near Site II traps. *Opuntia fragilis* (Nutt.) Haw. (pricklypear cactus) and *Centaurea maculosa* Lam. (knapweed thistle) grew on dry, overgrazed or barren lands. *Agropyron repens* (L.) Beauv. and *Poa spp*. were representative grasses close to Site II traps, also. *Stipa comata* Trin and Rupr. (needle and thread grass) was more scattered on the rangelands.

Site III traps were placed adjacent to suburban communities in the central part of the valley. Suburban areas had the widest diversity of exotic plant species associated with them. However, because the sites bordered towns, they also were next to the surrounding cultivated lands. The genera *Populus*, *Betula*, *Salix*, *Prunus*, *Malus*, *Pyrus*, *Rosa*, *Syringa* and *Acer* were well represented in suburban areas. *Lonicera utahensis* Wats. was frequently grown near homesites. As at the other site-types, bluegrass and quackgrass were the most numerous grasses surrounding the traps.

Site I Traps

Trap I-1. (T25N, R21W, S28) Elevation 3600 feet (1100 meters). The trap was set April 5, 1977 and removed August 15, 1977. This was the most northerly of all the traps, and it was on a steep south-facing slope above a 2-3 mile (3-5 km) wide, east-draining agricultural valley. South of the trap site, range and hay lands stretched up to the opposing side of the valley. North of the trap, and also on the opposing side of the valley, was montane forest. Numerous forbs around the trap included wild strawberry (Fragaria virginiana Duch.), sticky geranium (Geranium visco sissimum Fisch. & Mey.), cinquefoil (Potentilla sp.), horsemint (Monarda fistulosa L.), yarrow (Achillea millefolium L.), paintbrush (Castilleja hispida Benth.), lupine (Lupinus leucophyllus Dougl.) and arnica (Arnica cordifolia Hook.).

Trap I-2. (T22N, R19W, S19) Elevation 3400 feet (1037m). The trap was set April 4, 1977 and removed August 16, 1977. Toward the south this trap had an uninterrupted fetch across the valley. It was located at the apex of a mild east-west ridge (about 60-100m above the valley floor). North of the trap was coniferous forest on a north-facing slope down to the southern end of Flathead Lake. Immediately to the south of the trap was an alfalfa field (Medicago sp.).

Trap I-3. (T21N, R19W, S20) Elevation 3300 feet (1000m). The trap was set April 4, 1977 and removed August 15, 1977. Trap I-3 skirted the eastern extreme of the valley and it was open to the west, south and north. East of the trap was coniferous forest on a west-facing slope rising steeply into the Mission Mountains within about

4 km of the trap. Along an irrigation canal next to the trap were scattered cottonwoods and willows. Southwest of the trap was a barley field (Hordeum vulgare L.). Orchard grass (Dactylis sp.) was conspicuous here.

Trap I-4. (T18N, R19W, S29) Elevation 3200 feet (975m). The trap was set April 6, 1977 and removed August 17, 1977. This trap was southern-most of all the traps. Immediately south of the site was a dry wooded coulee containing numerous shrubs (hawthorn, chokecherry, willow, wild plum, elderberry, cottonwood). For 3-5 km further south was irrigated pasture land (Trifolium sp., Phleum sp., Medicago sp.) breaking into north-facing montane woodlands. North of the trap were spring wheat (Triticum sp.), barley, potato and hay fields and a wooded, shallow western drainage proceeded by more open agricultural lands (Fig. 1).

Site II Traps

Trap II-1. (T21N, R21W, S5) Elevation 2850 feet (870m). The trap was set April 5, 1977 and removed August 15, 1977. This trap was situated with open fetch from all directions. It was on bench land above the Flathead River. The river was about one mile (1-2 km) west of the trap and 150m below it. A dry unwooded coulee dropped to the west from the trap site down to the river. Grazing and rangeland surrounded the site. Some alfalfa and white clover occurred on irrigated land within 100 meters of the trap. Less than 10 isolated cottonwood trees grew by a rural homesite about 100 meters north of the trap.

Trap II-2. (T19N, R21W, S30) Elevation 2500 feet (750m). The trap was set April 6, 1977 and removed August 19, 1977. This trap was adjacent to a rural homesite on a bench about 15 meters higher than the Flathead River. Immediately to the south of the trap the land dropped into the river basin where irrigated pasture land preceded heavy shrub growth along the drainage. The genera *Crategus*, *Salix*, *Prunus*, and *Populus* predominated.

More irrigated pasture land, corn, potato and wheat crops were north of the trapping site. One to four kilometers toward the northeast an arid ridge about 50-100 meters higher than the trapsite separated the bench land from the central part of the valley. The residence near the trap may have affected prevailing winds from the east and west.

Site III Traps

Trap III-1. (T21N, R20W, S2) Elevation 3100 feet (950m). The trap was set April 5, 1977 and removed August 19, 1977. Trap III-1 was protected from northerly and easterly winds by scattered ponderosa pine trees and a residence. South of the trap site a small field (1-2 ha) of spring wheat was preceded by the town of Pablo. An alfalfa field was about 200m to the west of the trap. Near the residence by the trap grew a willow tree, plum and honeysuckle bushes.

Trap III-2. (T21N, R20W, S11) Elevation 3050 feet (930m). The trap was set April 4, 1977 and removed August 16, 1977. This trap was exposed to predominant winds from all directions except the northeast. A barley field was immediately to the west and an irrigated pasture was to the south. Northeast of the trap was the town of Pablo. Open, irrigated agricultural land predominated toward the south.

Trap III-3. (T20N, R20W, S2) Elevation 3000 feet (910m). The trap was set April 4, 1977 and removed August 15, 1977. A residence at the southwest edge of the town of Ronan was immediately northeast of trap III-3. A vacant lot of quackgrass turf preceded the first residence north of the trap. West, south and southeast a winter wheat crop grew. Open fetch afforded the trap from the west, south and southeast. Ronan's outdoor ornamental plants were the most diverse and abundant of all the Site III trapping sites.

Trap III-4. (T20N, R20W, S32) Elevation 2900 feet (880m). The trap was set April 4, 1977 and removed August 17, 1977. Although a residence was located 100 meters south of this trap site, prevailing winds were accessible to it from all other directions. To the southwest isolated cottonwoods and a few species of prunus accented semi-rural residences. The town of Charlo was about one-half kilometer south of the trap. Open, irrigated agricultural land surrounded the community. No woodlands were near to the site, and cultivated ornamental trees and shrubs were generally shorter and younger than those of other suburban trapping locales.

Trap III-5. (T19N, R20W, S5) Elevation 2900 feet (880m). The trap was set April 4, 1977 and removed August 17, 1977. This trap was placed on the east edge of a narrow, raised irrigation canal. A few Russian olive trees (Eleagnus angustifolia L.) less than 7-8m in height were growing on the east side of the canal and several meters north of the trap. A residence was immediately east of these. Open fetch preceded the trap from the west, south and east. Toward the northeast was the town of Charlo. Irrigated agricultural lands dominated the location. Orchard grass was conspicuous by the trap.

RESULTS AND DISCUSSION

Some aphids emerged from eggs prior to April 1, 1977 on Prunus virginiana L., Prunus cerasus L. and Crategus spp. Nymphs were observed near both trap site I-1 and I-4 in the first week of April. Nymphs were observed on Prunus domestica Marsh. in the last week of March in 1978 near trap site I-4. Aphids continued to hatch from eggs laid on chokecherry, hawthorn and plum until at least the middle of April.

The mean monthly maximum temperature attained 4°C for the 30-day period ending February 28 at both Polson and St. Ignatius. In Kalispell this value was reached for the 30-day period ending February 29. Aphid hatches appeared to initiate at least 2 weeks after these dates. By April 1 the preceding 30-day period had attained a mean maximum temperature of 6°C at both Kalispell and Polson and 7°C at St. Ignatius.

Hatching also appeared unrelated to the observed phenological dates within the valley. At the southern extreme of the study area the first bud of common purple lilac (Syringa sp.) leafed on April 7 and by April 10, 95% of the buds had leafed. At the northern end of the area these dates were delayed about one week. On April 13 the first bud had leafed near trap I-1 and by April 17 95% of the buds had leafed. In the south the first bloom appeared on May 1 and by May 23 95% of the blossoms had bloomed. Near to Site I-1 95% of the lilac blossoms had bloomed by June 2.

First instar nymphs observed on the terminal twigs of chokecherry were most frequently not present there two or three days later. Nymphs hatching from these egg sites at the tips of twigs and branches were consistently observed moving down them. Subsequently, colonies developed near the ground on new growth emerging at the base of chokecherry stands. Later, about 30% of the observed colonies were developing at the upper extremities of the stands.

Before the buds of chokecherry and hawthorn had opened, nymphs fed at the base of buds and on bud scales. After opening, the nymphs moved into the new florets and fed in protected locations of the florets and beneath bud scales. It was not until the appearance of the first generation of virginoparae that most nymphs on chokecherry moved onto young leaves to feed. This generation produced the first alatoid nymphs. These nymphs began to mature and to become flight-worthy in the third week of May. This observation was consistent with colony development on hawthorn, also, but colonies developed on the terminal twigs where hatching occurred. Fewer nymphs on hawthorn dispersed into the shrub stand.

A single observation of aphids on Prunus persicae L. at a central valley location revealed first and second instar nymphs on new buds in mid April. These gave birth to a generation of apterae. Both alatoid and apterous nymphs were deposited on the terminal twigs of peach by these apterae. These alatoid nymphs did not appear until the last week of May. The colonies were sprayed with a pesticide before the alates reached maturity.

Alates were numerous throughout the study area on hawthorn and plum in the first week of June. On chokecherry alatae appeared to migrate within one or two days of their final molt. Though alatoid nymphs were numerous within all observed aphid colonies on chokecherry, adult winged aphids were rarely observed on these shrub stands. Colonies on chokecherry remained active throughout the summer season. Those on plum and hawthorn had completed migrations from these hosts by the first week of July, though a few residual colonies remained on them throughout the season.

Whether due to predators or parasites, or to adverse weather, three out of seven observed stands of chokecherry displaying overwintering eggs and nymphs failed to give rise to aphid colonies. Likewise, two of three observed wild rose bushes failed to give rise to colonies though nymphs were observed on them in mid-April. The colony that did develop on rose was on a stand within a protected woodlot near trap I-2. The other two rose bushes were in open unprotected locales in the central and southern part of the study area, respectively.

A list of the aphid species identified from their overwintering hosts is given in Table 1, as confirmed by M. B. Stoetzel of the Systematic Entomology Laboratory at Beltsville, Maryland. These are in addition to the aphid species listed in Table 2, already identified from the Flathead Valley.[1]

Table I. Aphid species identified from their overwintering host plants in south Flathead Valley, Montana

Host Plant	Aphid Species
Plum *Prunus domestica* Marsh. *Prunus americana* L.	*Brachycaudus helichrysi* (Kltb) *Brachycaudus cardui* (L.) *Phorodon humuli* (Shrank)
Chokecherry *Prunus virginiana* L.	*Rhopalosiphum padi* (L.) *Rhopalosiphum sp.* possible cerasifoliae (Fitch)
Peach *Prunus persicae* L.	*Myzus persicae* (Sulzer)
Wild rose *Rosa sp.*	*Macrosiphum euphorbiae* (Thos.)
Hawthorn *Crategus chrysophyta* Ashe. *Crategus douglasii* Lindl.	*Acrythosiphon* sp. *Nearctaphis bakeri* (Cowen) *Nearctaphis crataegifoliae* (Fitch) *Rhopalosiphum nigrum* Richards

Table 3 shows the actual total aphid catches at each of the 11 trapping sites. An aphid catch from a single direction constituted one observation. These unadjusted catches are listed by date and site in Appendix B with the contribution of each catch to each 9-day interval. The adjusted aphid catches used for comparison between the trapping

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[1] O. G. Bain, 1976 & 1977, Environmental Management Division, Montana State Dept. Agriculture, 1300 Cedar Ave., Helena, Montana 59601. Personal communications.

Table 2. Aphid species identified from yellow pan trap collections in western Montana[1]

Acyrthosiphon sp.
Acyrthosiphon dirhudum (Walker)
Acyrthosiphon pisum (Harris)
Aphis sp.
Aphis craccivora Koch
Aphis fabae Scopoli
Aphis helianthi Monell
Aphis osetlundi Gillette
Brachycaudus cardui (L.)
Capitophorous braggi Gillette
Hyalopterous atriplicis (L.)
Macrosiphum sp.
Macrosiphum avenae (Fabricius)
Macrosiphum erigeronensis (Thomas)
Macrosiphum euphorbiae (Gillette)
Macrosiphum valerianae (Clarke)
Masonaphis sp.
Myzus persicae (Sulzer)
Nasonovia lactucae (L.)
Prociphilus americanus (Walker)
Rhopalosiphum maidis (Fitch)
Rhopalosiphum fitchii (Sanderson)
Sipha sp. possibly *agropyrella* Hille Ris Lambers

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[1] Courtesy O. G. Bain, 1977, Environmental Management Division, Montana State Dept. Agriculture, 1300 Cedar Avenue, Helena, Montana 59601, unpublished data.

sites and for analyses of variance are given in Appendix C. The adjusted total aphid catches at each site are given in Table 4 with also the adjusted arithmetic mean catch from each direction at each site.

Adjustments were made by dividing the number of aphids counted on the day of the trap check by the number of days since the last trap check. This number was then multiplied by nine, or the number of days in an interval. During any interval in which a trap was not checked a zero value was assigned and no data were included in calculations.

Table 3. Unadjusted total numbers of aphids trapped from each direction at each site and the actual mean catch at each site

Trap Site	Direction north	 east	 south	 west	Total	# obs.	Mean Catch
I-1	6	18	26	6	56	44	1.27
I-2	24	13	39	28	104	40	2.60
I-3	45	15	27	44	131	48	2.73
I-4	111	26	19	36	192	32	6.00
II-1	36	72	30	27	165	30	4.13
II-2	44	32	14	19	109	36	3.03
III-1	67	29	27	37	160	40	4.00
III-2	39	25	42	27	133	36	3.69
III-3	54	32	25	42	153	44	3.48
III-4	42	28	23	30	123	36	3.42
III-5	47	26	13	27	113	36	3.14
Total	515	316	285	323	1439		
Average	46.82	28.73	25.91	29.36	130.82		

At p = 0.01 for experimental error there was found no significant difference between the catches at Site I, Site II and Site III traps. Neither was there any significant difference between Site III trap catches and Site I and Site II trap catches. However, a Duncan's multiple range test (Snedecor and Cochran, 1968) on the least-squares means (Snedecor and Cochran, 1968) of the aphid catches at each site (Table 5)[1] revealed that the mean catches on trap I-1 and trap I-4 were significantly different (p = 0.01) from the mean catches on each

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[1] Discrepancies between these means and those given in Table 4 arise from the refined adjustments of the computer program to the unequal number of observations at the different sites and the least-squares computation method.

Table 4. Adjusted total numbers of aphids trapped from each direction at each site and the adjusted mean catch at each site.

Trap Site	Direction north	 east	 south	 west	Total	# obs.	Mean Catch
I-1	3.00	12.95	20.50	4.61	41.06	32	1.28
I-2	16.14	6.44	28.18	17.25	68.01	32	2.13
I-3	27.10	12.35	18.49	31.68	89.62	36	2.48
I-4	54.95	16.20	7.88	15.82	94.84	28	3.39
II-1	22.22	48.49	19.98	20.93	111.61	32	3.49
II-2	34.17	21.77	11.62	13.73	81.28	32	2.54
III-1	48.14	23.55	17.52	25.09	114.29	32	3.57
III-2	33.79	14.84	23.79	18.58	91.01	32	2.84
III-3	32.55	21.17	18.60	26.92	99.24	32	3.10
III-4	27.93	18.05	15.16	19.02	80.16	32	2.51
III-5	37.56	16.72	9.59	19.20	83.07	32	2.60
Total	337.55	212.52	191.30	212.82	954.18		

Table 5. Mean numbers of aphids trapped from each direction at each site calculated by the method of least-squares.

Trap Site	Mean Catch
I-1	1.29
I-2	2.13*
I-3	2.48*
I-4	3.59
II-1	3.49*
II-2	2.73*
III-1	3.57*
III-2	2.85*
III-3	3.10*
III-4	2.51*
III-5	2.60*

*At p = 0.01 for experimental error these values are not significantly different.

of the other traps. The mean catches on I-1 and I-4 not only reflected the extremes of the range of means but also the extremes of north-south range of trapping locations.

The total, unadjusted directional aphid catches are shown for each site, along with a summary of all the sites combined, in Figure 4. A least-squares analysis of the adjusted catches based on the method of unweighted means (Snedecor & Cochran, 1968) showed that directions were highly significant ($p = 0.01$) in the numbers of aphids trapped. A multiple range test on the least-squares mean catches from each direction showed that the number of aphids trapped from the north was significantly different ($p = 0.01$) than the number trapped from other directions. The mean catches from the east, south and west were not significantly different at $p = 0.01$ for experimental error (Table 6).

Whether or not prevailing winds influenced the significance of northerly trap catches was not positively determined. No official wind data was available from the study area, or within Lake County. From official wind data north of Flathead Lake, in Kalispell, the resultant wind direction in April, 1977 was southwest; in May, south; in June, west; in July, south-southwest; and in August, northeast (U.S. Dept. Commerce, 1977). The highest least-squares mean for aphid catches was during interval 11, in August (Appendix A). This supports the positive influence of wind in determining the high northerly trap catches. Of nine rural agriculturalists living within the study area, all stated

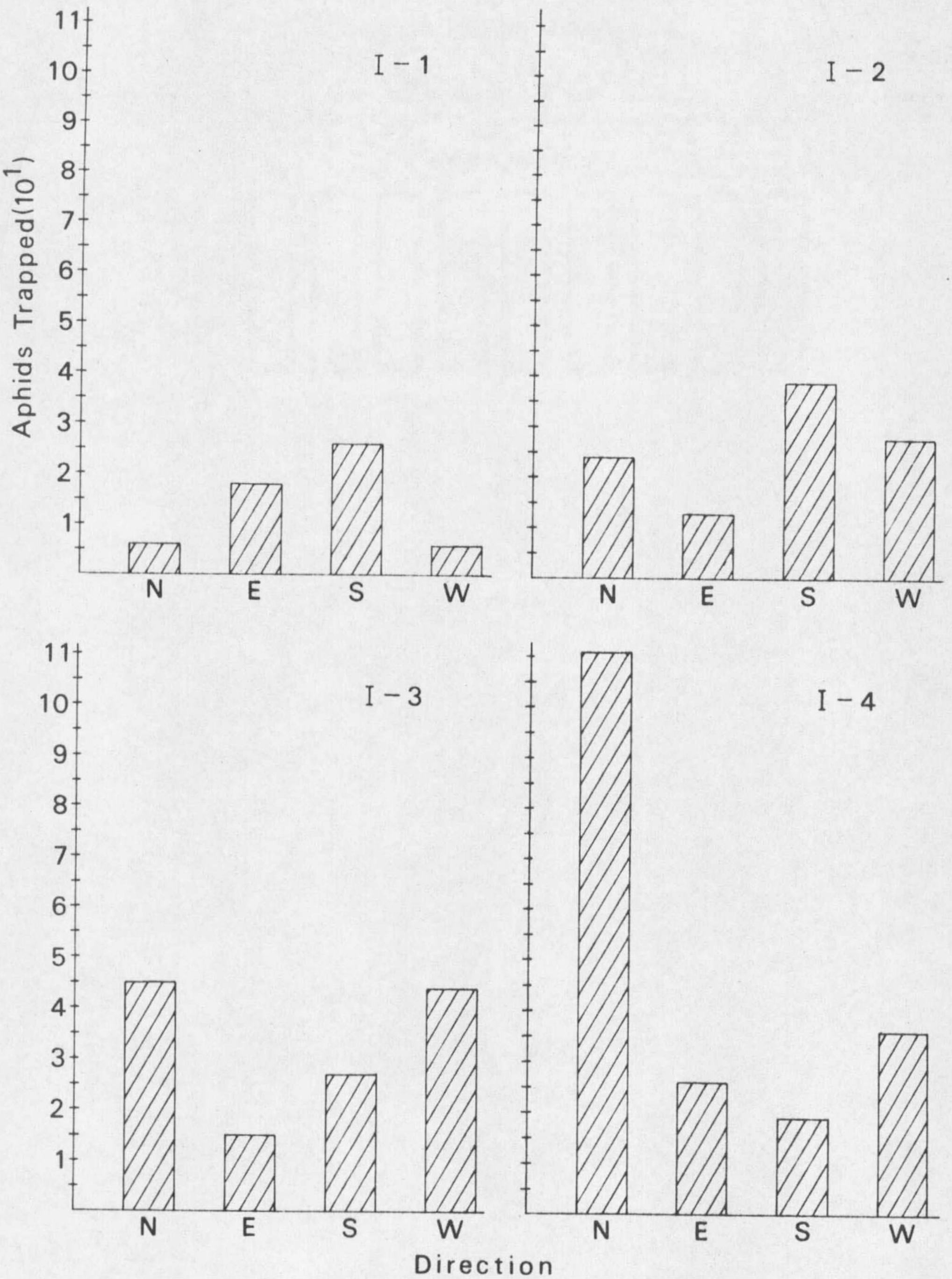

Figure 4. Histograms of the total unadjusted directional aphid catches at the 11 trapping sites.

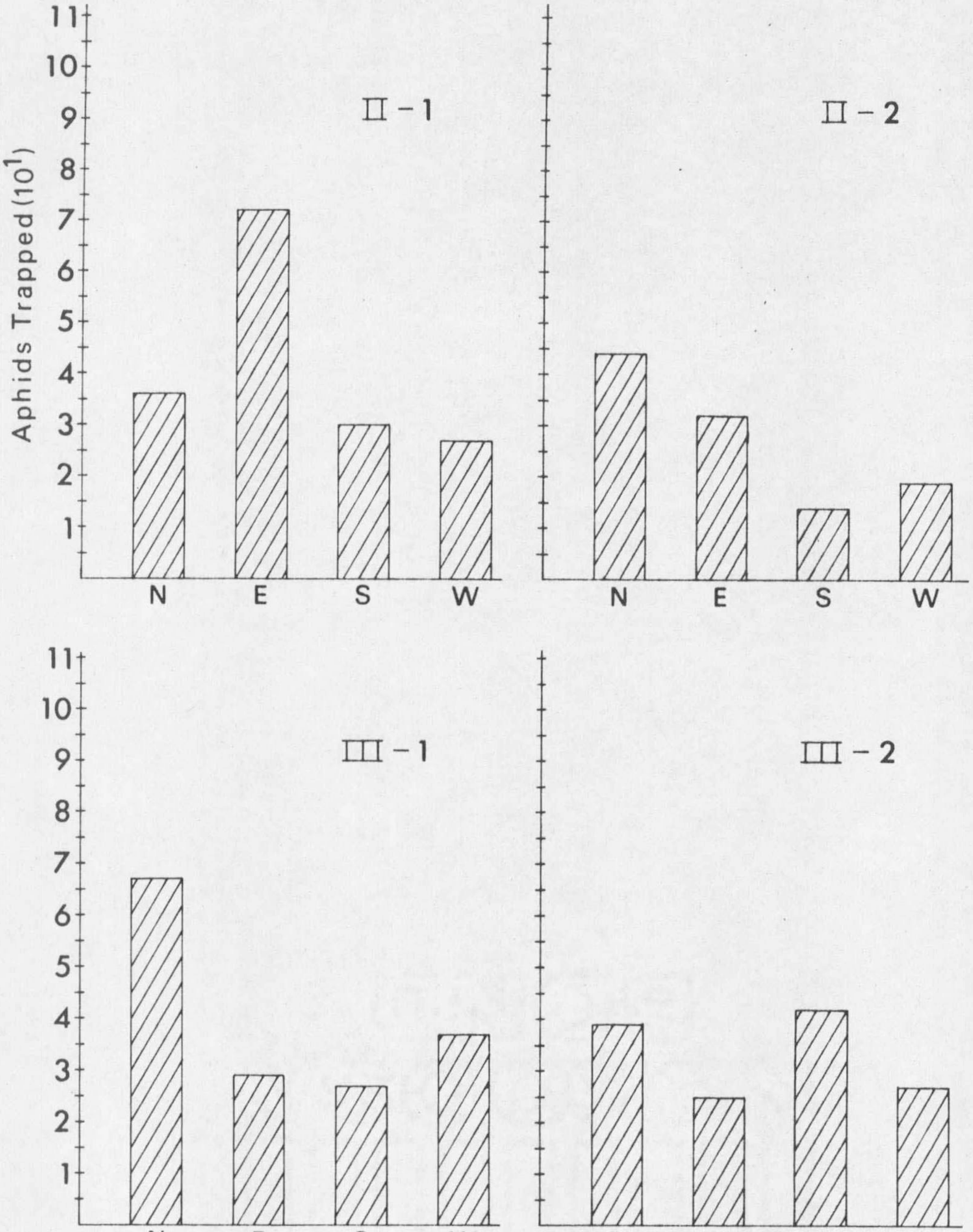

Figure 4 (continued).

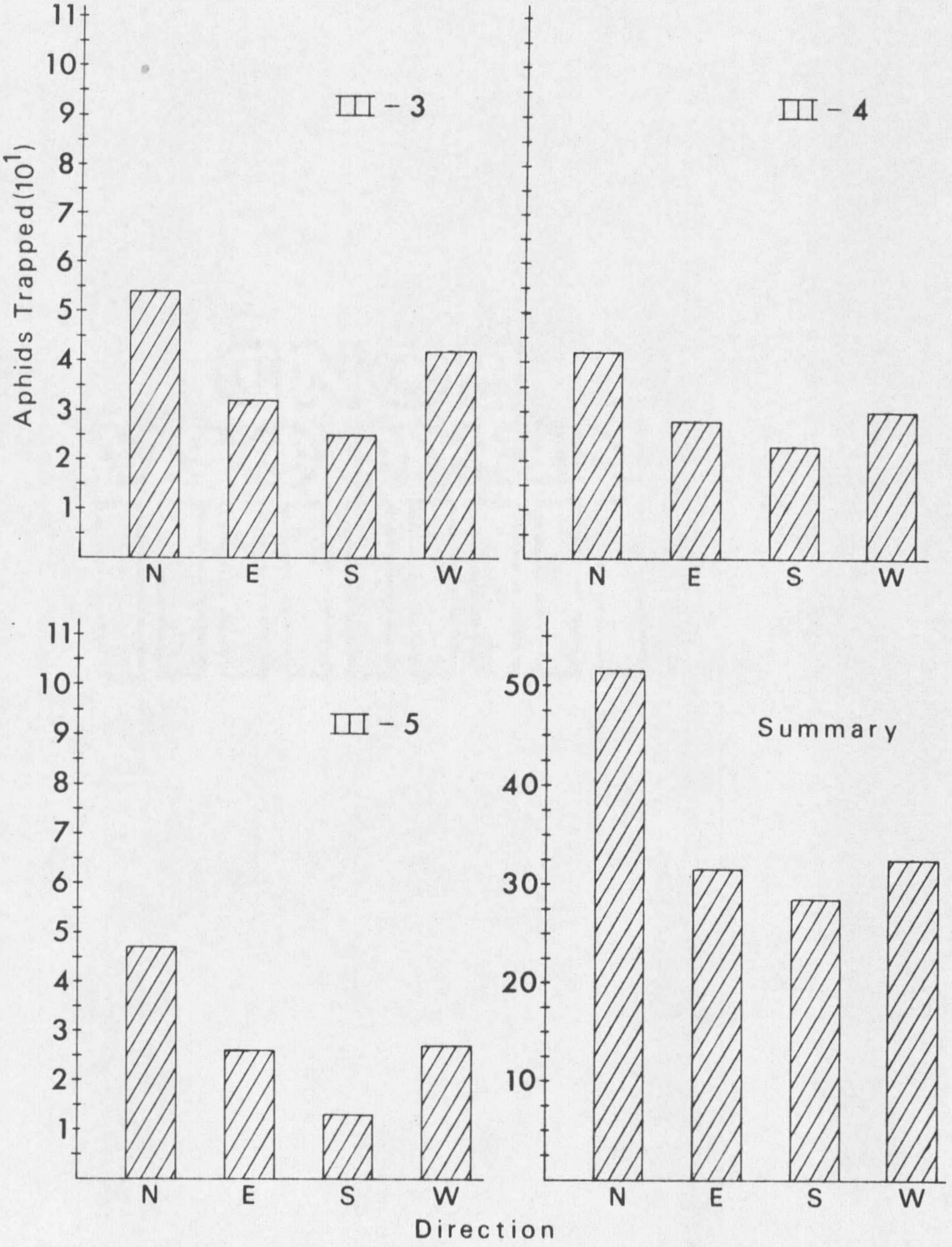

Figure 4 (continued).

Table 6. Mean trap catches from each direction at all sites combined, calculated by the method of least-squares.

Direction	Mean # Aphids Trapped per 9-day Interval per Direction
north	3.88
west	2.47*
east	2.46*
south	2.22*

*These values are not significantly different at the 1 percent probability level (p = 0.01) for experimental error.

that prevailing winds predominately blew from the west-southwest or from the north-northeast. And during the 1977 spring-summer season, they observed an inordinate amount of north-northeasterly wind. Wind appeared responsible for the significance of directional aphid catches.

An analysis of variance was computed for a curvilinear regression on the adjusted aphid catches from each trap,on the sum of the catches from all the traps, and on the combined catches from all the traps. Only the curvilinear regression for the combined catches from all the traps was significant (p = 0.01). This regression line is shown in Figure 6. The adjusted trap catches from each site and a mathematically interpolated summary of the adjusted catches are graphed in Figure 5.

In late June and during July of 1977, inspections of home gardens revealed only single aphids on garden crops. Numbers were few and inconsistent. In August of 1978, garden inspections revealed aphid

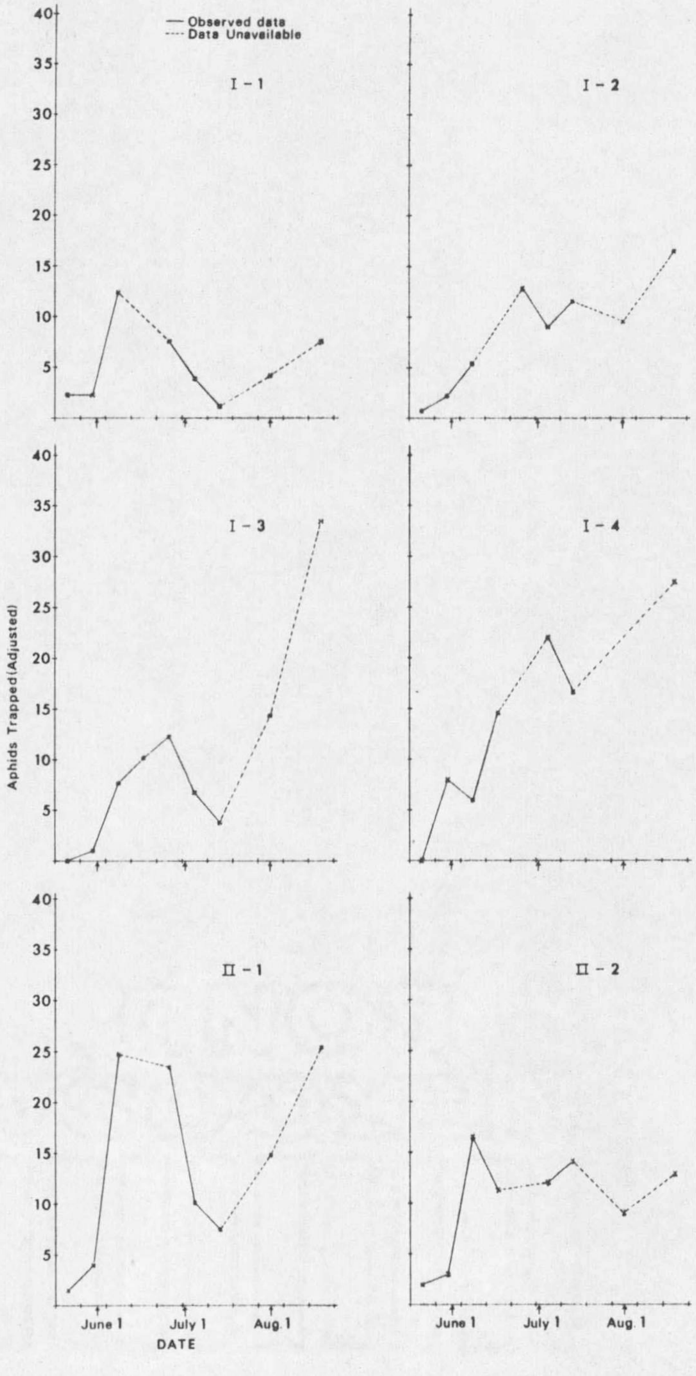

Figure 5. Adjusted aphid catches at the 11 trapping sites during spring and summer, 1977.

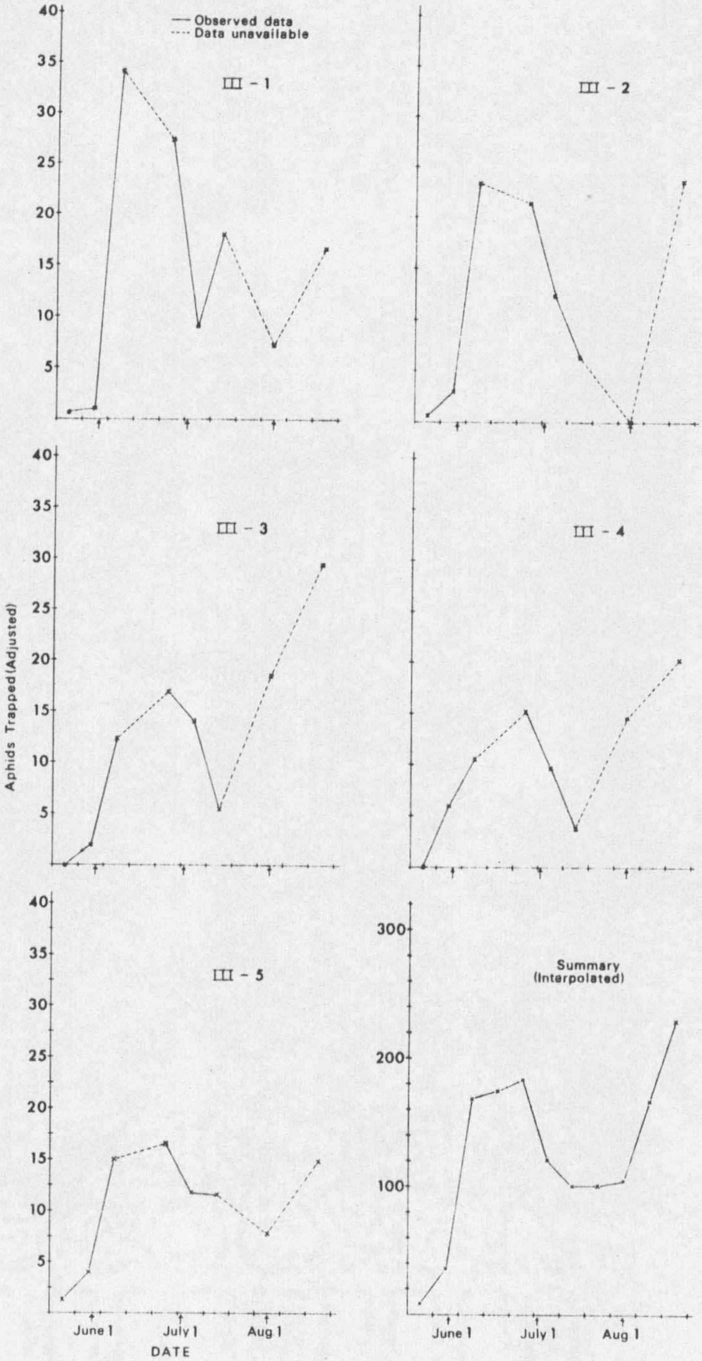

Figure 5 (continued).

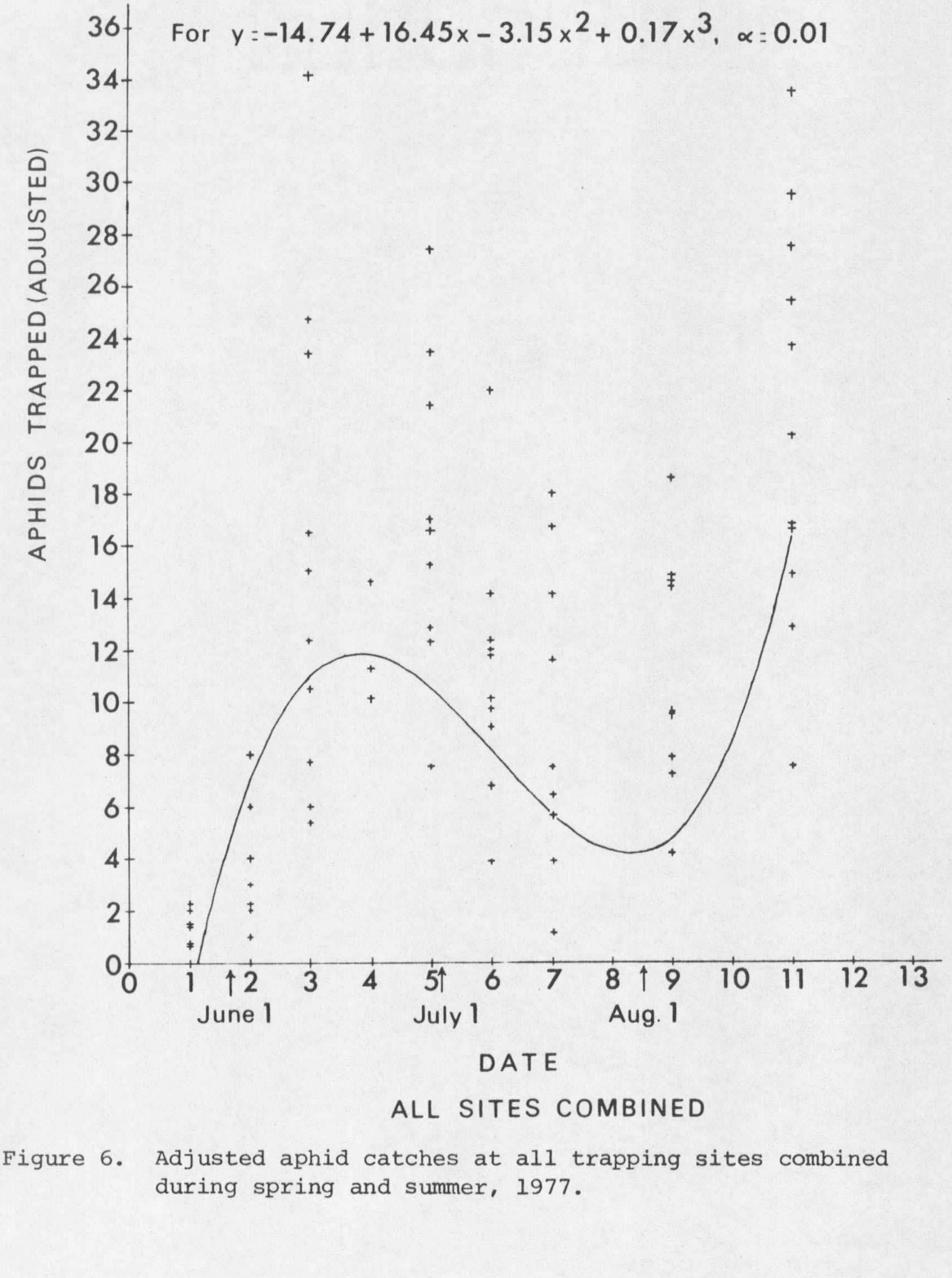

Figure 6. Adjusted aphid catches at all trapping sites combined during spring and summer, 1977.

colonies on broccoli, cauliflower, green pepper, tomato and potato plants. Alate peach aphids were most numerous on tomato, but apterous colony build-up was heaviest on green pepper. During this same period, alate peach aphids were observed near systemic insecticide-treated seed potato fields on volunteer potato plants and nightshade plants growing within a meter of the treated plants. Apterous peach aphids were infrequently present on the volunteer potato plants, and they were more frequent on nightshade plants. These inaggregate colonies were found scattered on the lowest leaves of plants, even when these leaves were heavily splattered and caked with silt. Symptomatic potato leafroll virus was also observed in potato and tomato plants in a few of these suburban home gardens.

Prunus spp. were invariably represented at both rural and suburban homesites. _Prunus persicae_ L. cultivation was predominantly confined to the vicinity of the lake, though peach trees were found at all extremes of the study area. At no location within the Flathead Valley were peach orchards observed. Peach trees at homesites and within cherry orchards usually numbered less than 10, and these were isolated. Inspection of about 50 peach trees in the community of

Polson on the south end of the lake during the spring of 1978 disclosed aphids that had overwintered as eggs.[1]

Summer insect surveys in irrigated clover, alfalfa and clover--containing hay pastures always revealed numerous aphids. Surveys of wheat, oat and barley fields, also always showed aphids present, though fewer than in hay and alfalfa fields. Both irrigated hay and grain fields were ubiquitous within the valley.

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[1] O. G. Bain, 1978, Environmental Management Division, Montana State Dept. of Agriculture, 1300 Cedar Ave., Helena, Montana 59601. Personal communication.

CONCLUSIONS

(1) The distribution of potato fields within the study area is primarily north central.

(2) The distribution of peach trees within the study area is predominately in the immediate vicinity of Flathead Lake though several isolated trees grow at homesites elsewhere in the valley.

(3) The distribution of secondary host plants of the aphid, *Myzus persicae*, is ubiquitous within the valley during spring and summer.

(4) Holocyclic populations of *Myzus persicae* overwinter in the study area on peach trees.

(5) Presently, *Myzus persicae* is not a widely abundant aphid within the study area during spring.

(6) The peak spring migratory period for aphids in the south Flathead Valley is mid and late June.

(7) Spring aphid flights are directionally significant and appear to be related to the prevailing winds.

(8) The primary reservoir of potato leafroll virus within the study area is believed to be potato and tomato plants in home gardens.

(9) Control of PLRV spread within the study area is dependent upon the distribution of source plants of the virus and the availability of overwintering hosts for the most efficient virus-vector, *Myzus persicae*.

APPENDIX

Appendix A. Adjusted mean trap catches during each 9-day interval from each direction for all sites combined, calculated by the method of least-squares.

Interval (date)	Mean Numbers of Aphids Trapped	a	b	c	d	e	f	g	h
11	5.19	a							
5	4.36	a	b						
3	3.82	a	b	c					
4	2.82			c	d				
6	2.74			c	d	e			
9	2.60			c	d	e	f		
7	2.28			c	d	e	f	g	
2	0.82							g	h
1	0.21								h

At $p = 0.01$ for experimental error, values marked with a letter in each column (a through h) are not significantly different. In each column (a through h) values with a letter present are significantly different from other values in the column.

Appendix B. Unadjusted aphid catches listed by site, date, direction and 9-day interval

Interval	Date	Direction				Total
		north	east	south	west	
Trap Site I-1						
	May 17, 1977	0	0	0	0	0
	5/20	0	1	0	0	1
1	5/25	0	0	1	0	1
2	6/2	0	2	0	0	2
	6/7	0	1	2	1	4
3	6/10	0	2	5	0	7
	6/22	1	4	2	0	7
5	6/28	2	3	3	0	8
6	7/5	0	0	2	1	3
7	7/13	0	0	1	0	1
9	7/28	0	2	3	2	7
11	8/15	3	3	7	2	15
	Total	6	18	26	6	56
Trap Site I-2						
	May 20, 1977	0	0	0	0	0
1	5/25	0	0	1	0	1
2	6/2	0	0	1	1	2
3	6/7	1	0	2	0	3
	6/22	3	5	6	10	24
5	6/28	1	0	4	1	6
6	7/6	0	0	5	3	8
7	7/13	4	0	3	2	9
9	7/28	3	4	7	2	16
11	8/16	12	4	10	9	35
	Total	24	13	39	28	104

Appendix B (continued)

Interval	Date	Direction				Total
		north	east	south	west	
Trap Site I-3						
1	May 24, 1977	0	0	0	0	0
2	6/2	0	0	0	1	1
	6/7	1	1	0	1	3
3	6/9	1	1	0	1	3
4	6/17	0	3	3	3	9
	6/22	5	0	0	3	8
5	6/28	2	1	2	2	7
6	7/6	0	0	3	3	6
7	7/13	0	1	0	2	3
9	7/28	8	3	6	7	24
11	8/15	28	5	13	21	67
	Total	45	15	27	44	131
Trap Site I-4						
1	May 25, 1977	0	0	0	0	0
2	6/3	1	5	0	2	8
3	6/9	3	0	1	0	4
4	6/17	7	3	1	2	13
6	7/5	29	5	4	6	44
7	7/12	9	2	0	2	13
11	8/17	62	11	13	24	110
	Total	111	26	19	36	192

Appendix B (continued)

Interval	Date	Direction north	Direction east	Direction south	Direction west	Total
Trap Site II-1						
	May 20, 1977	0	0	0	0	0
1	5/24	1	0	0	1	2
2	6/2	0	3	1	0	4
	6/7	1	8	2	0	11
3	6/10	2	6	2	1	11
5	6/28	14	12	11	10	47
6	7/6	1	0	1	7	9
7	7/12	1	1	1	2	5
9	7/29	5	11	7	5	28
11	8/15	11	31	5	1	48
	Total	36	72	30	27	165
Trap Site II-2						
	May 16, 1977	0	0	0	0	0
	5/23	1	1	0	0	2
1	5/25	0	0	0	0	0
2	6/3	2	1	0	0	3
3	6/9	5	2	2	2	11
4	6/17	3	3	3	1	10
6	7/5	7	5	6	6	24
7	7/12	6	2	1	2	11
9	7/29	5	6	1	6	18
11	8/19	15	12	1	2	30
	Total	44	32	14	19	109

Appendix B (continued)

Interval	Date	Direction				Total
		north	east	south	west	
Trap Site III-1						
	May 20, 1977	0	0	0	0	0
1	5/24	0	1	0	0	1
2	6/2	0	0	0	1	1
3	6/7	10	5	2	2	19
	6/22	18	10	11	5	44
5	6/28	2	0	5	13	20
6	7/6	1	2	2	3	8
7	7/13	5	3	2	4	14
9	7/28	7	1	1	3	12
11	8/19	24	7	4	6	41
	Total	67	29	27	37	160
Trap Site III-2						
	May 11, 1977	0	0	0	0	0
	5/21	0	0	0	1	1
1	5/24	0	0	0	0	0
2	6/2	1	1	1	0	3
3	6/7	10	1	0	2	13
	6/22	11	6	14	8	39
5	6/28	2	1	5	3	11
6	7/6	2	1	4	4	11
7	7/13	1	1	2	1	5
9	7/28	0	0	0	0	0
11	8/16	12	14	16	18	50
	Total	39	25	42	27	133

Appendix B (continued)

Interval	Date	Direction				Total
		north	east	south	west	
Trap Site III-3						
1	May 24, 1977	0	0	0	0	0
2	6/2	2	0	0	0	2
	6/7	3	1	0	2	6
3	6/10	1	2	2	0	5
	6/25	11	4	7	4	26
5	6/28	1	1	1	5	8
6	7/5	0	2	5	4	11
7	7/13	2	1	1	1	5
9	7/28	8	11	3	9	31
11	8/15	26	10	6	17	59
	Total	54	32	25	42	153
Trap Site III-4						
1	May 25, 1977	0	0	0	0	0
2	6/3	2	2	0	2	6
3	6/9	4	1	2	0	7
5	6/22	9	5	4	4	22
6	7/5	5	1	3	5	14
7	7/12	0	1	0	2	3
9	7/28	3	9	9	5	26
11	8/17	19	9	5	12	45
	Total	42	28	23	30	123

Appendix B (continued)

Interval	Date	Direction				Total
		north	east	south	west	
Trap Site III-5						
	May 12, 1977	0	0	0	0	0
	5/23	1	0	0	0	1
1	5/25	0	1	0	0	1
2	6/3	3	0	1	0	4
3	6/9	7	1	1	1	10
5	6/22	7	11	3	3	24
6	7/5	6	0	1	10	17
7	7/12	4	1	1	3	9
9	7/28	6	2	3	3	14
11	8/17	13	10	3	7	33
	Total	46	26	13	27	113

Appendix C. Aphid catches adjusted to 9-day intervals and listed by site and direction.

Date (interval)	Direction				Total
	north	east	south	west	
Site I-1					
1	0.000	1.125	1.125	0.000	2.250
2	0.000	2.250	0.000	0.000	2.250
3	0.000	3.375	7.875	1.125	12.375
4	0.000	0.000	0.000	0.000	0.000
5	1.500	3.500	2.500	0.000	7.500
6	0.000	0.000	2.571	1.286	3.857
7	0.000	0.000	1.125	0.000	1.125
8	0.000	0.000	0.000	0.000	0.000
9	0.000	1.200	1.800	1.200	4.200
10	0.000	0.000	0.000	0.000	0.000
11	1.500	1.500	3.500	1.000	7.500
	3.000	12.950	20.496	4.611	41.057
Site I-2					
1	0.000	0.000	0.750	0.000	0.750
2	0.000	0.000	1.125	1.125	2.250
3	1.800	0.000	3.600	0.000	5.400
4	0.000	0.000	0.000	0.000	0.000
5	1.714	2.143	4.286	4.714	12.857
6	0.000	0.000	5.625	3.375	9.000
7	5.143	0.000	3.857	2.571	11.571
8	0.000	0.000	0.000	0.000	0.000
9	1.800	2.400	4.200	1.200	9.600
10	0.000	0.000	0.000	0.000	0.000
11	5.684	1.895	4.737	4.263	16.579
	16.141	6.438	28.180	17.249	68.007

Appendix C (continued)

Date (interval)	Direction				Total
	north	east	south	west	
Site I-3					
1	0.000	0.000	0.000	0.000	0.000
2	0.000	0.000	0.000	1.000	1.000
3	2.571	2.571	0.000	2.571	7.714
4	0.000	3.375	3.375	3.375	10.125
5	5.727	0.818	1.636	4.091	12.273
6	0.000	0.000	3.375	3.375	6.750
7	0.000	1.286	0.000	2.571	3.857
8	0.000	0.000	0.000	0.000	0.000
9	4.800	1.800	3.600	4.200	14.400
10	0.000	0.000	0.000	0.000	0.000
11	14.000	2.500	6.500	10.500	33.500
	27.099	12.350	18.486	31.684	89.619
Site I-4					
1	0.000	0.000	0.000	0.000	0.000
2	1.000	5.000	0.000	2.000	8.000
3	4.500	0.000	1.500	0.000	6.000
4	7.875	3.375	1.125	2.350	14.625
5	0.000	0.000	0.000	0.000	0.000
6	14.500	2.500	2.000	3.000	22.000
7	11.571	2.571	0.000	2.571	16.714
8	0.000	0.000	0.000	0.000	0.000
9	0.000	0.000	0.000	0.000	0.000
10	0.000	0.000	0.000	0.000	0.000
11	15.500	2.750	3.250	6.000	27.500
	54.946	16.196	7.875	15.821	94.839

Appendix C (continued)

Date (interval)	Direction north	east	south	west	Total
Site II-1					
1	0.750	0.000	0.000	0.750	1.500
2	0.000	3.000	1.000	0.000	4.000
3	3.375	15.750	4.500	1.125	24.750
4	0.000	0.000	0.000	0.000	0.000
5	7.000	6.000	5.500	5.000	23.500
6	1.125	0.000	1.125	7.875	10.125
7	1.500	1.500	1.500	3.000	7.500
8	0.000	0.000	0.000	0.000	0.000
9	2.647	5.824	3.706	2.647	14.824
10	0.000	0.000	0.000	0.000	0.000
11	5.824	16.412	2.647	0.529	25.412
	22.221	48.485	19.978	20.926	111.610
Site II-2					
1	1.000	1.000	0.000	0.000	2.000
2	2.000	1.000	0.000	0.000	3.000
3	7.500	3.000	3.000	3.000	16.500
4	3.375	3.375	3.375	1.125	11.250
5	0.000	0.000	0.000	0.000	0.000
6	3.500	2.500	3.000	3.000	12.000
7	7.714	2.571	1.286	2.571	14.143
8	0.000	0.000	0.000	0.000	0.000
9	2.647	3.176	0.529	3.176	9.529
10	0.000	0.000	0.000	0.000	0.000
11	6.429	5.143	0.429	0.857	12.857
	34.165	21.766	11.619	13.730	81.279

Appendix C (continued)

Date (interval)	Direction				Total
	north	east	south	west	
Site III-1					
1	0.000	0.692	0.000	0.000	0.692
2	0.000	0.000	0.000	1.000	1.000
3	18.000	9.000	3.600	3.600	34.200
4	0.000	0.000	0.000	0.000	0.000
5	8.571	4.286	6.857	7.714	27.429
6	1.125	2.250	2.250	3.375	9.000
7	6.429	3.857	2.571	5.143	18.000
8	0.000	0.000	0.000	0.000	0.000
9	4.200	0.600	0.600	1.800	7.200
10	0.000	0.000	0.000	0.000	0.000
11	9.818	2.864	1.636	2.455	16.773
	48.143	23.549	17.515	25.087	114.294
Site III-2					
1	0.000	0.000	0.000	0.692	0.692
2	1.000	1.000	1.000	0.000	3.000
3	18.000	1.800	0.000	3.600	23.400
4	0.000	0.000	0.000	0.000	0.000
5	5.571	3.000	8.143	4.714	21.429
6	2.250	1.125	4.500	4.500	12.375
7	1.286	1.286	2.571	1.286	6.429
8	0.000	0.000	0.000	0.000	0.000
9	0.000	0.000	0.000	0.000	0.000
10	0.000	0.000	0.000	0.000	0.000
11	5.684	6.632	7.579	3.789	23.684
	33.791	14.842	23.793	18.582	91.009

Appendix C (continued)

Date	Direction				Total
(interval)	north	east	south	west	
Site III-3					
1	0.000	0.000	0.000	0.000	0.000
2	2.000	0.000	0.000	0.000	2.000
3	4.500	3.375	2.250	2.250	12.375
4	0.000	0.000	0.000	0.000	0.000
5	6.000	2.500	4.000	4.500	17.000
6	0.000	2.571	6.429	5.143	14.143
7	2.250	1.125	1.125	1.125	5.625
8	0.000	0.000	0.000	0.000	0.000
9	4.800	6.600	1.800	5.400	18.600
10	0.000	0.000	0.000	0.000	0.000
11	13.000	5.000	3.000	8.500	29.500
	32.550	21.171	18.604	26.918	99.243
Site III-4					
1	0.000	0.000	0.000	0.000	0.000
2	2.000	2.000	0.000	2.000	6.000
3	6.000	1.500	3.000	0.000	10.500
4	0.000	0.000	0.000	0.000	0.000
5	6.231	3.462	2.769	2.769	15.231
6	3.462	0.692	2.077	3.462	9.692
7	0.000	1.286	0.000	2.571	3.857
8	0.000	0.000	0.000	0.000	0.000
9	1.688	5.063	5.063	2.813	14.625
10	0.000	0.000	0.000	0.000	0.000
11	8.550	4.050	2.250	5.400	20.250
	27.930	18.052	15.159	19.015	80.155

Appendix C (continued)

Date (interval)	Direction				Total
	north	east	south	west	
Site III-5					
1	0.692	0.692	0.000	0.000	1.385
2	3.000	0.000	1.000	0.000	4.000
3	10.500	1.500	1.500	1.500	15.000
4	0.000	0.000	0.000	0.000	0.000
5	4.846	7.615	2.077	2.077	16.615
6	4.154	0.000	0.692	6.923	11.769
7	5.143	1.286	1.286	3.857	11.571
8	0.000	0.000	0.000	0.000	0.000
9	3.375	1.125	1.688	1.688	7.875
10	0.000	0.000	0.000	0.000	0.000
11	5.850	4.500	1.350	3.150	14.850
	37.560	16.718	9.592	19.195	83.066
Summary (Totals for all sites)					
1	2.442	3.510	1.875	1.442	9.269
2	11.000	14.250	4.125	7.125	36.500
3	76.746	41.871	30.825	18.771	168.214
4	11.250	10.125	7.875	6.750	36.000
5	47.161	33.324	37.768	35.580	153.833
6	30.115	11.639	33.644	45.313	120.711
7	41.036	16.768	15.321	27.268	100.393
8	0.000	0.000	0.000	0.000	0.000
9	25.957	27.787	22.985	24.124	100.853
10	0.000	0.000	0.000	0.000	0.000
11	91.839	53.244	36.878	46.444	228.405
	337.546	212.518	191.297	212.817	954.177

APPENDIX D - Potato Leafroll Virus

Distribution, Symptomology and Tissue Relations

Potato leafroll virus has a worldwide distribution wherever potatoes are cultivated. Host plants of the virus are mainly confined to the solanaceous family (Peters, CMI/AAB, 1970). Nightshade (*Solanum nigrum* L.), climbing nightshade (*Solanum dulcamara* L.) and tomato (*Lycopersicon esculentum* Mill.) are the most important alternate hosts of the virus (Dykstra, 1933) found in Montana. In some cases the nightshades acted as symptomless carriers of the virus, and occasionally tomato showed only slight stunting and outward expression of the infection (Dykstra, 1933). Other host plants not naturally occurring in Montana are *Amaranthus caudatus* L. (tropical tassel-flower), *Celosia argentea* L. (woolflower), *Gomphrena globosa* L. (globe amaranth) and *Nolana lanceolata* Meirs (Peters, 1970). Williams (1957) has shown the transmission of PLRV via the parasitic dodder plant, *Cuscuta inclusa* (*corymbosa* Ruiz. and Pav.). There also has been a single report of a graft transmission of the virus through a symptomless turnip (*Brassicae sp.*) to the President potato cultivar (Salaman et al., 1939). This report has not been confirmed. Host plants of the family brassicaceae are generally considered to be immune to PLRV (Helson and Norris, 1943).

Primary leafroll symptoms, those expressed in the same season as transmission occurred, rarely are observed because the minimum incubation period of the virus in field-grown potatoes is about a month.

However, under greenhouse conditions, secondary symptoms may develop in the same season of infection because of the artifically enhanced growing conditions (Whitehead and Currie, 1930). Symptoms include the upward rolling of leaflets around the midrib, a stiff erect appearance to plants and an interveinal yellowing of the leaves with random dead spots (necrosis). Infected plants nearly always show dwarfing and appear paler than healthy stock. Lower leaves of the plant are always rolled, though sometimes only slightly, and have a leathery, brittle texture, frequently dying back from their tips. A slight reddish cast along the upper leaf margins is sometimes observed. Current season symptoms include leafrolling and yellowing (chlorosis) in the uppermost leaves. These symptoms are sometimes confused with a Rhizoctonia fungal infection, but this disease produces brown lesions on the potato stems. Leafroll infections produce no stem discolorations (McKay et al., 1933).

Yields from diseased plants are significantly reduced, and the tubers are few and clumped close to the stem (McKay et al., 1933). Harper et al. (1975) have classified the symptoms of PLRV on the basis of yield reduction. Slight symptoms produce 65% yield reduction, moderate symptoms 80% reduction, and severe symptoms about 92% yield reduction. Infected tubers appear normal on the surface, but sometimes show a network of brown strands or dead tissue originating from the stem-end when the tubers are cut open (net necrosis) (Hodgson et al., 1974). Infected tubers produce long spindly sprouts even when net necrosis has not developed (Rich, 1968).

Webb et al. (1951,1952,1955) distinguished five strains of PLRV and determined their relationships by differential symptom expression on the common test plants, Datura strammonium L. (jimson weed) and Physalis floridana Rydb. (groundcherry). P. floridana proved diagnostic for even mild strains of the virus (Manzer et al., 1977). Severity of infection with these strains was correlated with the amount of chlorosis and stunting exhibited by test plants. A South Dakota strain has appeared to be the most severe. Webb et al. (1952) also reported that potato infection with an avirulent strain of leafroll virus protects plants from infection with a virulent strain. An aphid-vector of PLRV carrying both virulent and avirulent strains was able to transmit the virulent strain as readily as an aphid carrying only one strain (Harrison, 1958).

As soon as PLRV-infected potato plants unfold their first leaves, they respire at much higher rates than healthy plants (Whitehead, 1934). Water loss from these plants is higher than normal, initially, but later an abnormal water balance develops from a reduction in the number of functional stomata (Merkenschlager and Klinkowski, 1929). A retardation of enzymatic activity in diseased tissue results in the incomplete hydrolysis of starch to sugar and an overall accumulation of starch (Ruhland and Wetzel, 1933). Infected tubers contain fewer auxins than healthy tubers (Sequeira, 1963). All the soluble nitrogen fractions of potato plants except ammonia and asparagine are increased by leafroll infections, but the interference of the virus with tuber expansion is not due to a shortage of normal translocates (McDonald, 1976). Nitrogen-treated plants infected with leafroll generally grow healthier with less symptom expression and are preferred by aphids for feeding and colonizing (Kassanis, 1952). The addition of potassium nitrate to infected plants increases their yield slightly at 15°C in the first year, but the progeny of these plants are unaffected by the treatment in the second year at either 15°C or 20°C (Butler and Murray, 1932).

Leafroll virus particles observed within the potato plant with the electron microscope were restricted to the phloem cells (Kojima et al., 1969). Because of this limited range of the virus within the plant, natural inhibitors of the virus in other plant tissues were found to be ineffective in preventing infection. This is also a reason for the inability of the virus to be spread by mechanical inoculation (Bawden, 1955). The aphid vector inoculates the virus directly into the phloem cells where it feeds, bypassing the tissues where natural virus inactivators reside.

The virus is inactivated when held at 70°C for 10 minutes. It survives in extracted plant sap 4 days at 2°C but only 12-24 hours at 25°C in aphid extracts (Peters, 1970). The virus in infected tubers is inactivated after 20 days when the tubers are held at 36°C or above, but whole plants and their tubers remain infected after the same treatment. This has been suggested as a treatment for seed stocks to keep them free of the virus (Kassanis, 1957).

The leafroll virus particles are more or less hexagonal isometric particles of about 23 nanometers in diameter (Peters, 1967) and contain a double stranded DNA (Sarkar, 1976). This separates the leafroll virus from all other types of potato viruses and allies it more closely with the caulimoviruses (Gibbs and Harrison, 1976) than with the luteoviruses with which it was previously associated.

Sarkar (1975) has devised a routine diagnostic method for identifying the virus within a few hours by concentrating the virus particles from homogenates of sprouting potato tubers with ultracentrifugation. Casper (1977) found that the roots of potato plants contain the highest concentrations of potato leafroll virus and are also suitable as a virus source for purification. He was able to prepare an antiserum specific for PLRV that detected the virus particles by enzyme-linked immunosorbent assay (ELISA). In comparison to other viruses PLRV attains very low titres in its hosts, even in the most suitable ones.

Transmission of PLRV through true seed (Dittmer, 1964) has not been shown and is considered doubtful (Peters, 1970).

PLRV Within Its Aphid Vector

The acquisition threshold time, or the length of time an aphid vector needs to probe and to feed upon a PLRV-infected source plant to acquire the virus, is generally less than one hour (Kassanis, 1952). However, Woodford (1973) has observed that non-viruliferous vectors of PLRV rarely acquired the virus when they fed for less than 2 hours on infected potato plants. Peters (1973) suggested that the acquisition time is better defined as not just the time when the virus was taken into the gut, "but when it starts circulating through the body from the lumen." This was based on Ponsen's (1970) finding that transmission efficiency of PLRV was increased by a starving period. The vector frequently retains its infectivity for 3-4 weeks or its entire life (MacCarthy, 1954). The infecting power of the aphid is retained through the molt of the insect (Elze, 1931). After being imbibed by the aphid the virus passes from the alimentary canal to the haemolymph and may be observed in the fat cells and honedew of the insect with the electron microscope (Ponsen, 1972). Thence it passes into the salivary glands (Peters, 1973) from where it is transmitted to suitable host plants with the saliva of the phloem-feeding vector. The virus is transmitted in a minimum of 2.5 minutes (transmission threshold time) and can be acquired in a minimum of 1.6 minutes of feeding time (acquisition threshold time)(Leonard and Holbrook, 1978). With an electronic monitoring system, EMS, these authors found a direct relationship between the duration of the acquisition feed and the probability of the aphid becoming infective and pathogenic. The latent period between imbibition and inoculation can be 6-12 hours (Day, 1955). There has been a report of the ability of the virus to be transmitted without a latent period, and within an hour of a 30-minute acquisition feed (Kirkpatrick and Ross, 1952).

Harrison (1958) found that aphid vectors injected with extracts of other aphids that were allowed long feeding periods on PLRV-infected source plants had a higher transmission efficiency than aphids injected with extracts of short-feeding-period viruliferous aphids. Likewise, Peters (1973) found a marked increase in transmission ability with increased acquisition feeds of aphids. Both authors, on this evidence suggested that PLRV did not multiply within its aphid vector. Sugawara et al. (1973) suggested that, because they found the virus latent period increased as the injected virus dosage decreased and because the virus concentration within the aphid gradually decreased after leaving a source plant, no matter how long the acquisition feeding period, the virus only circulated and accumulated in the blood of the insect but did not multiply. Therefore, vector blood was responsible for retention of inoculativity. They found that infectivity was dependent upon the dosage of virus acquired. Their attempts to maintain virus inoculativity with serial passages of viruliferous aphid extracts, or blood, to other aphids were unsuccessful.

Contrarily, Day (1955) reported that the ability of the vector to transmit PLRV was not proportional to the acquisition period and that the frequency distribution of the number of infections plotted against the duration of the inoculation-feed followed an exponential curve. He concluded that the virus did multiply within the vector, though to a limited extent. Stegwee and Ponsen (1958) and Ponsen (1972) shared a similar view. Observing that the dilution end point of the haemolymph of viruliferous aphids was 10^{-4} for PLRV, they carried the virus through 15 serial passages in which the dilution of the virus would have been diminished to 10^{-21}. The final recipient aphids of the virus were infective. They suggested that the increase of virus concentration within the vector was dependent upon the amount of insect egestion, and that the demonstration of virus decrease in concentration, per se, could not be considered conclusive evidence against virus multiplication within the vector. Limitations of detection techniques for PLRV have inhibited thorough investigation of this topic. For a more complete discussion the reader is referred to Peters (1973).

Miyamoto and Miyamoto (1966) were able to show transovarial passage of leafroll virus to a small percentage (about 1%) of second generation nymphs. Infective nymphs were more frequently produced at low temperatures than at high ones. They found no correlation between the appearance of infective nymphs and the duration in which maternal aphids were reared on infected leaves. A second attempt by the same authors to show transovarial passage at a later date failed (Miaymoto and Miyamoto, 1971). A virus that passed easily through other tissues also was thought able to move into ovarial tissues (Black, 1959). The passage of virus from oviparous aphids to their eggs has not been reported.

Table 7 shows the known aphid vectors of PLRV and those species identified from the Flathead Valley of northwestern Montana. Subimaginal apterous nymphs have been found to be the best vectors of PLRV. Very young nymphs are the weakest vectors and adults are intermediate (Kirkpatrick and Ross, 1952). Adults are better vectors when they are reared on infected plants (Kirkpatrick and Ross, 1952).

PLRV and Its Hosts in Relation to Their Environment

The environment influences the degree and expression of symptoms and the rates of virus spread (Schultz, 1923). Transmission is the outcome of a sequential process: (1) acquisition of virus by the vector, (2) survival of infectivity during the association of virus and vector, (3) inoculation of virus into plants, and (4) the initiation of infection (Gibbs and Harrison, 1976). The environment influences the interaction of these factors.

Doncaster and Gregory (1948) found that the amount of PLRV incidence from sources more distant than an adjacent field was usually slight compared to spread from plants already infected within the

Table 7. Known aphid vectors of potato leafroll virus

Acyrthosiphon solani Elze, 1927; *Myzus pseudosolani* Murphy and M'kay 1929; Hille Ris Lambers, 1933; *Myzus solani* (Kaltenbach), 1843.

***Aphis fabae* Scopoli, 1763.

***Aphis nasturtii* Kaltenbach, 1843; *A. rhamni* Loughane, 1943.

***Macrosiphum euphorbiae* Gillette and Palmer, 1934.

Myzus ornatus Loughnane, 1939.

***Myzus persicae* (Sulzer), 1776.

***Myzus humuli* Heinze, 1960; *Phorodon humuli* Gillette and Palmer, 1934.

Myzus ascalonicus Doncaster, ; Rhopalomyzus, Heinze, 1952.

Neomyzus circumflexus Smith, 1931; Myzus, Heinze, 1960.

Rhopalosiphoninus latyisiphon Roland, 1952.

Rhopalosiphoninus staphyleae Heinze, 1959; *Hyzotoxoptera tulipaella*, 1960

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*J.S. Kennedy, M.F. Day, and V.F. Eastop. *A Conspectus of Aphids as Vectors of Plant Viruses*. Commonwealth Agricultural Bureau, The Eastern Press, Ltd., 1962. 114pp.

**Species identified from the Flathead Valley of northwestern Montana (Bain, O.G., 1977, Environmental Management Division, Montana State Dept. of Agriculture, 1300 Cedar Ave., Helena, Montana 59601).

field. Of primary importance in virus spread are alate aphids that move through the crop early in the season. The static populations of aphids that develop are dependent upon weather and crop conditions. The occurrence and distribution of PLRV and its vectors has no relationship to temperature and precipitation (Bishop, 1965). Bishop (1965) found the highest incidence of PLRV occurring in fields adjacent to suburban-urban areas. No fields more than 5 miles (8 km) from towns had heavy PLRV-infected vector infestations. He suggested home gardens as the infection source of the virus. There is "little evidence that potato viruses are carried between crop seasons in alternate hosts (besides potato), at least in the north temperature climate" (Bagnall, 1977). Flower and vegetable transplants import vector colonies. Broadbent (1950,1965) found also that most PLRV spread was by alates and that at least half of the leafroll spread occurred early in the season before apterous populations built up. This early season virus spread occurred when aphids were few. Little virus spread was observed later in midseason when aphids were numerous (Heathcote and Broadbent, 1961). Knutson and Bishop (1964) reported that twice as many plants and four times as many tubers became infected with PLRV before July 15 as afterwards in Idaho. Infections from winged aphid inoculations result in more partially infected potato hills than with apterous aphid inoculations (Broadbent and Tinsley, 1951). Virus infections spreading from sources outside the crop occur at random in fields and in a district where aphid vectors were not numerous, Clinch et al. (1938) found it possible to maintain potato stocks free from viruses by moderate commercial isolation. Early harvesting of seed plots has been recommended for the control of PLRV spread (Rich, 1968). Orienting fields away from wind sources likely to bring in migrating aphids also has produced some control of disease spread (Hodgson, 1974).

Arenz and Hunnius (1959) found that the susceptibility of potato plants to leafroll infection decreased as plants approached flowering due to the change from the vegetative stage of growth to the reproductive phase. Occasionally, current season symptoms are produced from inoculations before the middle of July, but post-July 15 inoculations produce no symptoms in the first year (Knutson and Bishop, 1964). The percentage of tubers becoming infected decreases with the age at which the plant is inoculated. Knutson and Bishop (1964) found that when only one tuber from a hill was indexed for PLRV, 35% of the infected tubers went undetected; in 3-7-tuber hills there was found an 18% greater frequency of infection in the largest tuber than in the remaining tubers. Using larger tubers (110 gms plus) for indexing increased the likelihood of leafroll detection. Five to 10 days after inoculation of the potato plants, the virus can pass into some of the tubers and 16 days after inoculation it can infect all the tubers within a hill (Bradley and Ganong, 1953).

Young PLRV-infected plants are better inoculant for aphids than older plants with pronounced symptoms. The best inocula are earth-breaking, symptomless plants (Kassanis, 1952). Aphids feeding on lower leaves of flowering potato plants cause more infections than those feeding on middle leaves or buds (Kirkpatrick and Ross, 1952).

The acquisition of a second virus by an aphid vector does not adversely affect its ability to transmit leafroll virus (MacKinnon, 1961). MacKinnon (1961) suggested also that not only should the species of the source plant upon which the aphid vector was reared be considered when comparing the aphid's vector efficiency, but also whether or not this host was infected with other unrelated viruses.

Potato Resistance to Virus and Vector

Potato leafroll infections in potato growing areas of the northeastern United States have tended consistently upward in the 1970s. Slightly resistant potato cultivars like Katahdin and Kennebec have shown a gradual increase in their susceptibility to leafroll. Natural selection tends to produce resistant cultivars among plants. In alternate hosts, potato viruses are found to be naturally resisted and rejected (Bagnall, 1977). But crowded pure stands of moderately resistant crop varieties are believed to be no more capable of resisting a disease than more susceptible varieties in the mixed and scattered conditions of nature (Holmes, 1955).

Resistance to PLRV is of a general, non-specific type (Bagnall, 1977). Several authors have reported high inoculation resistance to PLRV in some potato cultivars (Clark, 1963; Gregor, 1963; Webb and Hougas, 1959). There is some resistance to virus increase and spread in selected, or bred, cultivars already in use (Hamann, 1961). Improvement of existing resistance to PLRV has been demonstrated in diploid and tetraploid potato cultivars (Bagnall, 1977).

Hutton (1949), after observing the different degrees of phloem necrosis in potato cultivars inoculated with PLRV, suggested breeding potato cultivars hypersensitive to leafroll virus. No results were cited.

On the potato cultivars Bintje, Katahdin, Kennebec, Kerr's Pink, King Edward, Majestic, and Pentland Crown, reproductive rates of the green peach aphid, Myzus persicae (Sulzer), are below observed laboratory rates on other cultivars (Mackauer and Way, 1976). Most aphid resistant potato cultivars are found from diploid and tetraploid potato species, and their resistance varies with different aphid species (Radcliffe and Lauer, 1971a,1971b; Tingey and Plaisted, 1976). This resistance is controlled by may genes and is of a non-specific type (Lower, 1974). These resistant genotypes show little interaction with environmental factors in the field (Sams et al., 1975). While these cultivars provide protection from aphid colonization and damage (Blackman, 1976), it is difficult to cross them with commercially more suitable potato cultivars and to pass on the resistant qualities (Sams et al., 1977). Because Myzus persicae does not form dense aggregate colonies on most of its hosts and because potato is not a preferred host for the peach aphid, dramatic alteration of the aphid as a vector can be obtained by breeding only limited increases in potato resistant to the aphid.

APPENDIX E - Myzus persicae (Sulzer): Vector Biology

Host Selection, Insecticides and Biological Control

Although Myzus persicae has been shown to be the vector of 50 different plant viruses, its specificity for different viruses has not been satisfactorily explained (Smith, 1977). Adaption between a virus and an aphid is most likely when both share a common host plant, but virus spread is less likely among the most favored, highly specific host plants of aphids than among less favored ones. Polyphagous aphids tend to be better vectors because they have many hosts and no highly specific ones (Kennedy et al., 1962). Aphids apread viruses among hosts they do not colonize (Heinze, 1959). Aphids with wide host ranges, however, respond more to the physiological conditions of the host than monophagous or oligophagous aphid species (Kennedy et al., 1962).

The selection of young and aging leaves of suitable hosts occurs as an optomotor response to yellow by winged aphids (van Emden, 1969). The stimuli for host selection by an aphid are received through the stylets, after they have penetrated the substrate, rather than through the antennae, rostrum or tarsi (Wensler, 1962). Food quality affects the larval development of the peach aphid, and the amount of sap imbibed by the young nymphs varies markedly with the food's nutritive value (Harrewijn and Noordink, 1971). The amount of food uptake by

Myzus persicae has been positively correlated with the amino acid methionine and the total amide concentration in plant sap (Mittler, 1970). The amount of amide in potatoes is closely affected by the type and rate of fertilization. Growth rate of the green peach aphid has also been positively correlated to increased methionine titre in plants (Blackman, 1976).

Phelan et al. (1976) showed that aphids mechanically disrupted from settled colonies oriented towards vertical objects at least 75% of the time, and that aphids dislodged by alarm pheromone showed a decreased orientation toward vertical objects and an increased locomotion rate. The condition of the colony affected dispersal to other nearby plants by disrupted individuals.

Four hundred and seventy-three secondary host plants of Myzus persicae have been identified in the Rocky Mountain region. Host plants occurred most abundantly within the Families Apocynaceae, Bigoniaceae, Caprifoliaceae, Compositae, Leguminosae, Malvaceae, Myrtaceae, Rosaceae, Rutaceae, Scrophulariaceae, Solanaceae and Verbenaceae (Leonard and Walker, 1970). Heathcote (1962) found that peach aphids developed better on species of Brassicae (turnip and mustard) than on beets, spinach and lettuce, and that the suitability of these hosts changed with their maturity. Reproductive performance of the peach aphid changed as much as a factor of four on different secondary hosts. The degree of adaptation of an aphid to a plant is measured best by the aphid's ability to colonize all plant parts in different stages of development (Kennedy et al., 1950). The build-up of polyphagous aphid populations is influenced most by the species of host plant and its condition, particularly if the host is an unfavorable one for the aphid (van Emden and Way, 1973). This is very important in the population dynamics of the peach aphid because the peach aphid has not been found to form dense aggregate populations on most of its secondary hosts (Blackman, 1976).

Tropic biotypes of aphid populations may arise from the prolonged effect of changes in their life conditions (Shaposhnikov, 1961). These aphid populations are not equivalent to each other in their relationship to food plants (Muller, 1958). Trophic adaptions are considered an initial stage in the formation of forms, but the frequency with which these adaptions occur has been found to be dependent upon the degree of selection pressure and the suitability of the hosts (Shaposhnikov, 1961).

Insecticides are in common usage for the control of aphid populations and the viruses they spread. Carbofuran, Methamidophos, and NRDC 143 (synthetic pyrethroid similar to Endosulfan) are relatively new aphicides that have shown good experimental control of aphids (Campbell and Finlayson, 1976). Granular systemic insecticides are widely used because they are applied to the soil and are absorbed by plants over a long period (Close, 1967). Disulfonton and Phorate have been shown to significantly reduce aphid colonies and to inhibit the aphid's ability to colonize plants for at least 10 weeks (Matthews, 1970). Rizvi et al. (1976), in a one month study, found Phorate, Aldicarb, and Disulfoton of relatively equal efficiency in reducing and keeping down populations of Myzus persicae, and Bacon et al. (1976) obtained the best insecticide control of aphid populations using Aldicarb in combination with Monitor foliar sprays. However, the latter observed the Disulfoton granules with 1-3 aerial applications of Disulfoton, Endosulfoton, Demeton, Oxydemetonmethyl, or Parathion frequently gave no control of peach aphid in and around potato fields. Wolfenbarger (1972) observed that foliar sprays were frequently unsuccessful in cold weather. Sprays applied at temperatures within the thermal optimum of the peach aphid (13°-19°C) gave near 90% kills, but at 10°C only 80% of the aphids were killed, and at 7°C only a 67% kill was obtained.

Some peach aphid populations from nearly all of 35 field sites in Britain have shown degrees of resistance to organophosphorus insecticides (Devonshire and Needham, 1975; Devonshire et al., 1977; Sykes, 1977). Some of these are considered highly resistant. Dunn and Kempton (1977) also observed a greenhouse 'strain' of Myzus persicae that persisted when sprayed to run-off with Demeton-S-methyl. This strain also was unaffected by a furrow application of Disulfoton granules. These authors suggested that it was more feasible for resistant aphids to establish themselves in the field from greenhouses than by direct migration of alates. Organophosphorus-resistant aphid populations (biotypes[1]) have shown a homogeneous morphology with respect to specific characters that make them distinct from 'normal' populations (Eastop and Russell, 1967).

While insecticides reduce and control aphid populations, they do not kill viruliferous aphids quickly enough to prevent the transmission of potato leafroll virus (Till, 1971). Bacon et al. (1976) found no correlation between the populations of apterae that built-up on insecticide treated plots and the incidence of PLRV-infected plants and tubers in the plots. They concluded that although infection with PLRV was highest in years of greatest aphid populations, its incidence appeared to be correlated more with the numbers of winged aphids. Insecticides offered no protection from viruliferous alate aphids, and the futility of attempting to control PLRV on an individual field basis with insecticides was suggested. Resistant clones of aphids, in general, are less fit than wild types, and natural selection tends to eliminate them unless insecticides interfere with population interactions (Baker, 1977).

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[1] "Biotypes are recognizable by biological function more than morphology or karyotype" (Blackman, 1976), and they "are inherent in the aphids' way of life" (Mackauer and Way, 1976).

Mineral oil applications to crops provide at least a 50% reduction in the transmission of non-persistent viruses (Simons et al., 1977). Its action is effective for 6 days during 150% leaf expansion and up to 32°C. The oil accumulates over the anticlinal walls of the epidermal cells (Simons and Beasley, 1977) where aphids normally initiate probes (Bradley, 1963). The oil increases the aphid's pre-probing time and inhibits the ingestion of sap. Vanderveken and Dutrecq (1970) found transmission inhibited in all cases where contact of the aphid stylets and the oil was established.

Predators are found to be most important in controling peach aphids when they occur in high numbers early in the season before the maximum rate of increase is attained by aphid populations (Blackman, 1976). The predator impact is most significant on potatoes. More predators are found in potato fields adjacent to wooded areas than elsewhere (van Emden, 1969). Maximum mortality rates occur after aphid populations reach their peak, when predators are numerous, but predators are considered an unlikely cause of population decline at this time (Blackman, 1976).

Decreases in green peach aphid populations resulting from parasites and disease appear to be small (Blackman, 1976). Aphidophagous fungi are active only near 80% relative humidity and emerge through the insect's cuticle only when the relative humidity reaches 90% at night

(Rockwood, 1950). Fungicides have been shown to reduce the numbers of diseased aphids in test plots, and there is evidence that they protect aphids from infection by entomogenous fungi (Nanne and Radcliffe, 1971). Of 30 parasites studied by Mackauer and Way (1976), none were specific to peach aphids or preferred them over other species. Economically acceptable biological control of the green peach aphid by enhancing natural enemies is not feasible after the aphid has reached the potato crop (Mackauer and Way, 1976).

Population Biology

DeLoach (1974)(Fig. 7) established some of the population growth parameters for the green peach aphid, and these are comparable to the findings of Weed (1927)(Table 8). DeLoach found the aphid's maximum rate of increase was 1.32 per day at 25°C. At this rate, populations doubled in 2.5 days. Peak net reproduction (R_o) was attained at 20°C, at which temperature the aphid populations increased a maximum of 29 times per generation. For all the species he studied, mortality was greater when the populations were young. Whitehead (1931) found the speed of nymphal development of Myzus persicae increased with increasing temperatures from 10° to 29°C. Body length and width increased slightly in successive generations reared at 10°C, and fecundity was highest at 25°C.

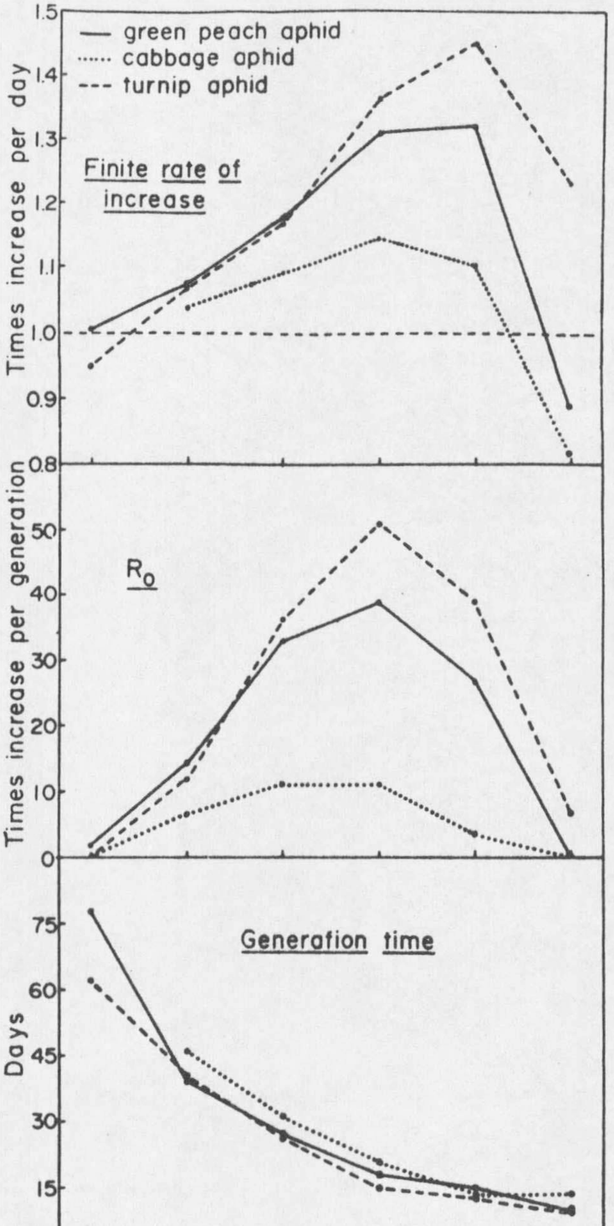

Figure 7. Finite rate of increase (λ), net reproductive rate (R_o), and length of generation (T) for Myzus persicae and two other aphid species (reproduced by permission of the Entomological Society of American from the Annals of the Entomological Society of America, Volume 67, p. 336, 1974).

Table 8. Metamorphosis, reproduction and longevity in apterous forms of <u>Myzus persicae</u> (Sulz.) as influenced by temperature and humidity (reproduced by permission of the Entomological Society of America from the Journal of Economic Entomology, Volume 20, p. 156, 1927).

METAMORPHOSIS

Chamber	Individuals	Hours between birth and 1st molt			Hours between 1st and 2nd molts			Hours between 2nd and 3rd molts			Hours between 3rd and 4th molts			Hours between birth and maturity			Length of instars in hours			Hours between maturity and prod. of 1st nymphs		
		Max.	Min.	Aver.	Max.	Min.	Aver.	Max.	Min.	Aver.	Max.	Min.	Aver.	Max.	Min.	Aver.	Max.	Min.	Aver.	Max.	Min.	Aver.
I 10°-60%	16	192	48	126.00	144	96	120.00	144	120	126.00	168	120	129.00	624	456	501.00	192	48	125.25	144	48	86.40
II 16°-65%	22	96	48	75.27	96	48	67.63	120	48	60.00	120	48	70.90	360	192	273.80	120	48	68.45	72	12	34.66
III 21°-70%	138	72	24	47.44	72	24	49.21	72	24	48.34	72	24	54.96	240	144	199.95	72	24	49.98	72	12	27.15
IV 24°-75%	67	72	24	39.04	72	24	38.33	72	24	34.03	72	24	44.42	192	120	155.82	72	24	38.95	48	12	22.00
V 28°-85%	8	48	24	36.00	48	48	48.00	48	24	36.00	72	48	54.00	192	168	174.00	72	24	43.50	48	12	24.00

REPRODUCTION AND LONGEVITY

Chamber	Individuals	Actual reproduct. Period in days			Young produced daily								Longevity in days								
					Average based on				Total				Nymphal			Adult			Total		
		Aver.	Max.	Min.	Reproductive period	Adult longevity	Max.	Min.	Aver.	Max.	Min.		Aver.	Max.	Min.	Aver.	Max.	Min.	Aver.	Max.	Min.
I 10°-60%	12	25.25	32	17	1.79	1.45	5	1	45.25	57	36		21.66	26	19	31.25	41	26	52.91	61	46
II 16°-65%	18	20.50	26	15	2.62	1.88	8	1	53.83	83	16		12.10	15	8	28.50	41	19	40.60	53	31
III 21°-70%	36	17.66	24	10	3.23	2.56	10	1	57.11	85	18		8.38	10	6	22.28	41	11	30.66	48	19
IV 24°-75%	24	16.00	20	12	3.72	3.00	10	1	59.62	75	40		6.23	8	5	19.87	30	13	26.00	37	20
V 28°-85%	12	7	9	5	3.07	1.95	8	1	21.5	37	6		7.33	8	7	10.50	14	8	17.83	20	14

In comparison to some of its secondary-host-related species, apterous populations of the peach aphid have a faster rate of increase between 5° and 15°C, and are the only populations that are able to increase at 5°C (DeLoach, 1974). This is evidenced by Figure 8 which shows the developmental rates of *Myzus persicae* and *Macrosiphum euphorbiae* Thomas by temperature regime. *M. euphorbiae* infestations are frequently associated with peach aphid infestations, and the latter are enhanced by slight infestations of the former (Duncan and Couture, 1957). *M. euphorbiae* out-performs *M. persicae* on potatoes (Mackauer and Way, 1976) even though its immature mortality rates are higher and its apterous fecundity rates are lower than the peach aphid (Barlow, 1962). Barlow (1962) also showed that populations of *M. euphorbiae* produced 70% alates while *M. persicae* only produced 1%.

Poor light ($\underline{\underline{\bullet}}$800 lux) has been shown to reduce the fecundity of the peach aphid, and photoperiod appears to have no general effect on population growth, though it has complex interactions with other factors (Wyatt and Brown, 1977). Fluctuating temperatures increase the rate of aphid development over the rates observed from constant-temperature rearing in the laboratory (Siddiqui et al., 1973). Bishop (1965) found that peach aphids developed best at high temperatures on shaded, heavy vine growth, and that populations developed rapidly on exposed potato vines during cloudy weather. Rain and hard winds can diminish peach aphid populations 50% on potatoes (Shands et al., 1956). Cool

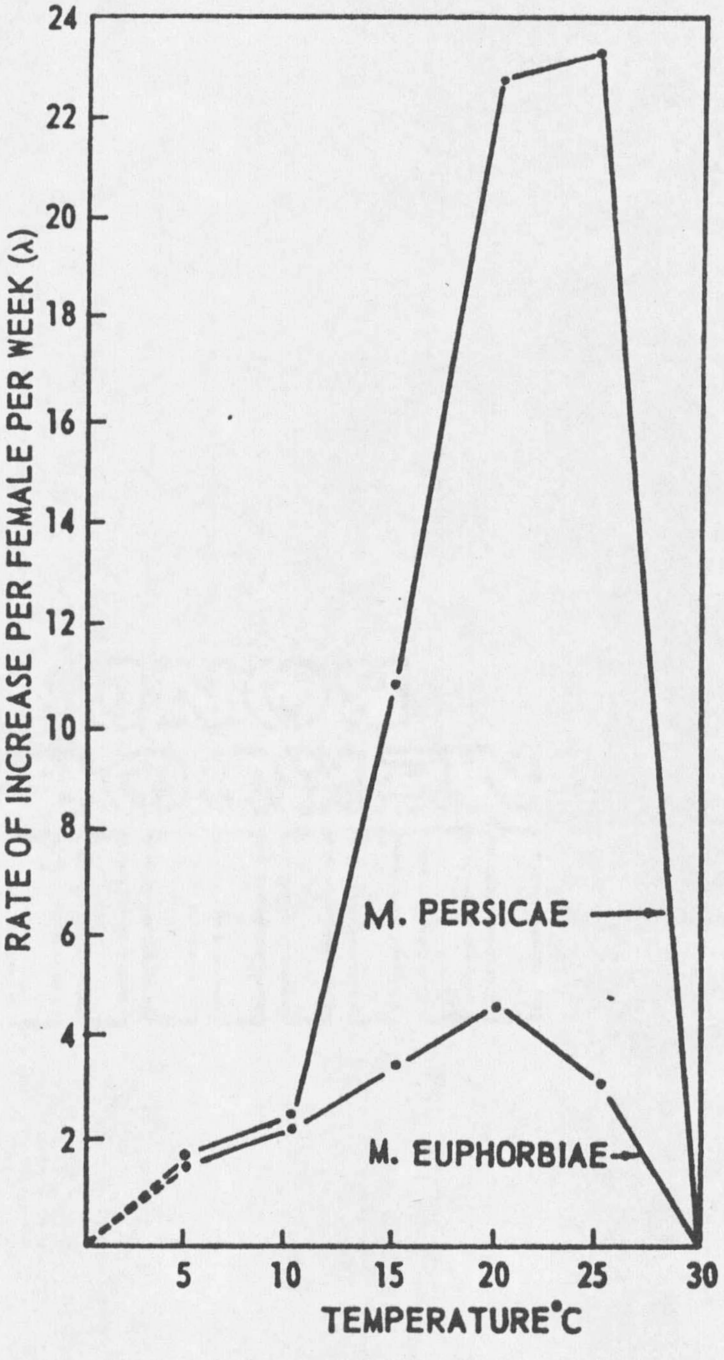

Figure 8. Finite rates of increase of Myzus persicae and Macrosiphum euphorbiae at constant temperature from 5°C to 30°C (reproduced by permission of the National Research Council of Canada from the Canadian Journal of Zoology, Volume 40, p. 152, 1962).

conditions produced by local weather variations, increased elevation or increased latitude decrease aphid infestations and delay their approach to peak densities (Fisken, 1959).

Hurst (1965) found wet winters and springs associated with light virus incidence. Predictions of virus incidence based on local weather records have not been very useful and require consistent records of aphid population dynamics over a long period (Watson et al., 1975).

Data from 10 countires between the north latitudes of 37° and 56° indicate that the stadia of the peach aphid are functions of a constant number of day-degrees (Blackman, 1976). Its intrinsic rate of increase is determined by a method outlined by DeLoach (1974). The predictive model method he used provides a basis for defining regulatory factors for populations in the field. Mortality is determined by measuring the difference between two field observations of increase rates. Though found to be valid between 10° and 25°C, the model is more accurate at low temperatures.

Davies and Landis (1951) studied the biology of the peach aphid in Washington on peach trees. They observed the hatching of fundatrigeniae in the last two weeks of February or the first two weeks of March. In the Flathead Valley this date appears to be delayed about two weeks. In Washington the stem mother developed in about 29 days and had a one to two month longevity. Its reproductive period lasted an average of 19 days during which it produced an average of 4 young per day. Each generation developed faster than the preceding one from the egg to the seventh generation. Winged spring migrants were produced in the third generation, and one surviving aphid represented 400 winged aphids in the third generation.

Shaposhnikov (1959) stated, "In obligate heteroecious and obligate diapausing species a firmly established number of spring generations predetermines (irrespective of environmental factors) the onset of migrations . . ." He suggested migrants as specialized forms incapable of feeding and multiplying on their primary host under any condition. Mackauer and Way (1976) affirmed that winged viviparous peach aphids from secondary hosts and winged fundatrigeniae from peaches were unable to reproduce on _Prunus persicae_ L.

Female fall migrants (gynoparae) of _Myzus persicae_ attempt to colonize a wide variety of primary hosts, but seldom are successful except on _Prunus persicae_ and _P. nigra_ L. (van Emden, 1969). Even overwintering on other species of prunus seldom is successful because the progeny of stem mothers develop poorly except on peach and apricot (Palmer, 1952).

Eradication of aphid overwintering hosts has helped to control potato virus spread (Steinbauer and Steinmetz, 1945). Powell and Mondor (1976) obtained a 60% reduction in May-June peach aphid populations with an alternating insecticide spray program on peach trees every two years for two years' duration. After two years of spraying, they obtain a 3-11% reduction in tuber net necrosis from indexed fields and observed a 10-43% reduction in chronic leafroll incidence.

In Washington, the first winged gynoparae arrived to peach trees in mid and late September and deposited oviparous nymphs that matured and began egg deposition by mid October. Arrival of winged males was synchronized with maturation of oviparae. Oviparae developed on leaves, then moved onto twigs to mate (Tamaki et al., 1967). Males were attracted by the sex attractants of the oviparae rather than by the host plant (Kennedy et al., 1959). The oviparae are unable to feed or develop on peach after it becomes dormant (Ward, 1934). Oviparae reaching maturity lay 4-13 eggs.

In warm weather, overwintering aphid eggs have similar survival rates on both exposed and protected egg sites. However, in very cold weather more eggs die in protected locations than in exposed ones because soil and vegetation at protected sites remain frozen longer (Lewis and Siddorn, 1972).

Remigration to the primary host is stimulated by autumn decreases in photoperiod and lowering temperature (Shaposhnikov, 1959). Daiber and Scholl (1959) found the critical photoperiod for the production of peach aphid sexuales was greater than 11.3 hours and could be replaced by a critical temperature of about 18°C. In France, a 12.5 to 14-hour photoperiod triggered production of gynoparae, and 12.5-13.5 hours of daylight stimulated male production (Bonnemaison, 1951). Blackman

(1975) produced alates and males in the f_2 generation and oviparae in the f_3 generation by exposing the parental generation to a 10-hour photoperiod at 20°C from their fourth instar period inwards. Previously, the parents were under a 16-hour daylength. Interclonal variation in photoperiodic response was cited (Blackman, 1971).

Myzus persicae frequently survives mild winters in the apterous condition if the mean temperature in the three coldest months exceeds 4°C (van Emden, 1969). These anholocyclic populations retain their ability to produce sexuales even in conditions where holocycly is impossible (Scholl and Daiber, 1958). Scholl and Daiber (1958) also found that in warm temperate and tropical climates, where photoperiod did not induce sexual production, sexuales occasionally were produced at higher altitudes despite long photoperiods.

In eastern Washington, overwintering of the green peach aphid is mainly holocyclic, but anholocycly has been reported (Davies and Landis, 1951). Colorado has reported holocyclic overwintering (Berry and Simpson, 1967). In Idaho, only holocycly has been found, but in Minnesota and Manitoba, Canada, little or no outdoor overwintering occurs, and infestations of Myzus persicae are thought to occur from migrants from farther south (Mackauer and Way, 1976). Both holocycly and anholocycly were found occurring in California with holocycly more prevalent in northern regions of the state. Anholocycly was reported in sheltered situations in British Columbia, Canada, while holocycly predominated in the colder interior of the province (Wright et al., 1970). Oklahoma populations are mainly anholocyclic (Walton, 1954). Anholocyclic populations in Arizona show year-round flight activity (Coudriet and Tuttle, 1963).

Mackauer and Way (1976) have discussed the occurrence of androcyclic populations of green peach aphid populations that are predominantly anholocyclic but produce males feebly. This trait has been suggested as recessive to holocycly and heritable (Blackman, 1972) (Fig. 9). These clones produce males nearly three times more efficiently on the brassicaes as on potatoes. This trait was also found in association with the fragmentation of one or two chromosomes of the normal complement (Blackman, 1976). A reciprocal translocation between two autosomes, associated with organophosphorus resistance to insecticides, was found as the chromosomal variant of androcyclic clones in greenhouses. A similar, or identical translocation heterozygote has been reported from Japan in holocylic populations (Blackman, 1976).

Because the green peach aphid is feebly adapted to most of its secondary hosts, it is very susceptible to the physiological differences in these hosts. Whether trophic or otherwise, control measures exert pressure for genetic change and control is best when it considers both the manifested and the potential genetic flexibility of the aphid. Biotypic variants are naturally resisted in the absence of any control measures. Successful artificial control of the peach aphid

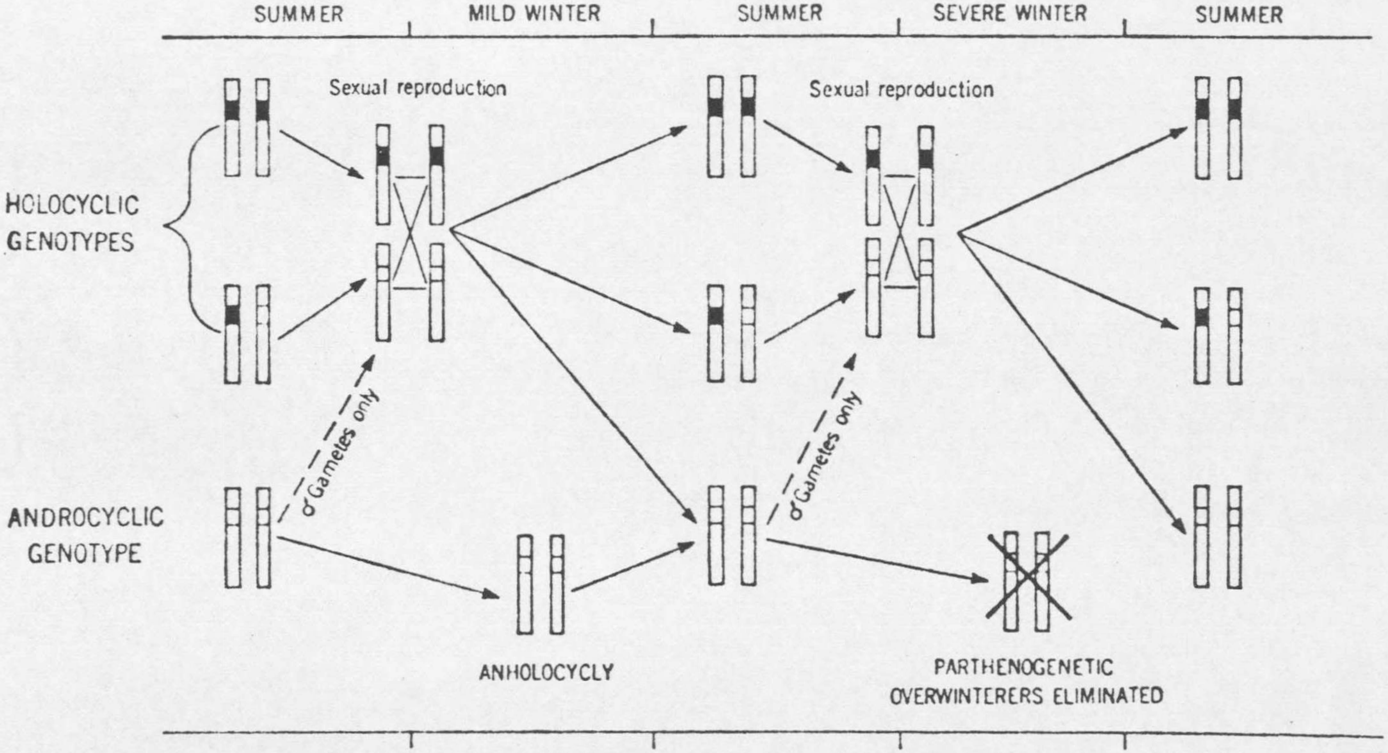

Figure 9. Maintenance of life-cycle variation in Myzus persicae through three seasons. Androcyclic clones are generated afresh by the breeding system each year, even after a severe winter when parthenogenetic morphs outdoors are eliminated (reproduced by permission of the Cambridge University Press as publishers of Studies in Biological Control edited by V. L. DeLucchi).

like natural controls, is dependent upon no single cause of mortality but several integrated ones (Kennedy et al., 1962; Blackman, 1976; Mackauer and Way, 1976; Baker, 1977).

Flight Ecology

Migratory flight has not been found to be concomitant with the alate condition (Dry and Taylor, 1970). Flight ability varies within and between populations and among different ages of alates (Johnson, 1976). Aphids are considered more 'normally' apterous (with wing rudiments), and the alate condition represents a diversion from this basic form (Applebaum et al., 1975).

Juvenile hormone has no apparent effect on apterous production in the green peach aphid (Applebaum et al., 1975). Thymidine is highly significant for wing determination in the aphid (Raccah et al., 1973).

Woodford and Lerman (1974) noted eight inclusive morphological characters that separated spring migrants of the peach aphid produced on primary hosts from those produced by anholocyclic populations. The latter migrants are found present earlier in the season than holocyclic spring migrants (Howell, 1973). Spring migrants from primary hosts remain flight-worthy longer than alates produced on secondary hosts, however, and they require longer flight times before settling (Woodford, 1968). Initial virus infections in potatoes result from spring migrants and subsequent spread is usually from within crops or from adjacent fields (Bradley and Rideout, 1953; Lamb and Close, 1961). Trapping programs detect these migrants before they reach crops (Taylor, 1973). Because Myzus persicae is found to be a widely dispersing species, only a few traps are required to evaluate dispersal patterns over wide ranges (Blackman, 1976). Fields adjacent to peach orchards are infested earlier in the season with higher numbers of peach aphids, and these are trapped at crop level (Davies and Landis, 1951). High positive correlations between trap catches of Myzus persicae and the incidence of PLRV in potatoes have been reported (Hollings, 1955).

Taylor (1965) differentiated two types of aphid flights; phase I flights in which aphids are not attracted to plants and initially fly at great heights (up to 1500 meters), and phase II flights in which aphids fly near to or within the boundary layer, alight on plants, deposit nymphs and usually fly again. Phase I flights are more numerous among spring migrants. Generally, most migration takes place in windy weather (Johnson, 1954). However, in wind speeds greater than 1.5 miles per hour (2.5 km/hr), flights are largely uncontrolled (Swenson, 1968).

Atmospheric mixing governed by temperature lapse rates that affect the size and patterning of convection currents over vegetation govern aphid dispersal. Atmospheric temperature gradients fluctuate by diurnal and seasonal cycles. These are correlated with vertical gradients of aphid distribution (Johnson, 1957). The minimum temperature for aphid flight was found by Swenson (1968) to be 15.5°C. The timing of migrations and the survival of aphids between them is determined mostly by the weather (Taylor, 1977). Taylor (1977) also found mortality during host finding was from hundreds to thousands of individuals per one success, but resource finding by Myzus persicae is considered very efficient in comparison to most other species.

Woodford (1973) found that Myzus persicae was flightworthy and active for 4-5 days even though it had settled on a suitable host plant. Johnson (1976) reported that prolonged flights occurred early in adult life and were subsequently shorter with age. He also observed that flight muscles histolyzed in a day or two after the first flight, but that flight ability could be prolonged for two weeks in darkness. This indicated that longer flight ability occurred under cloudy conditions. In finding that most trapped aphids were making their first flight, Johnson (1956) suggested that most aphid flights were limited in duration, too. Cockbain et al. (1963) observed that initial flights of about 2 hours induced settling in the peach aphid. Though flight take-off is inhibited in light below 100 footcandles (Broadbent, 1949), aphids appear to remain in the air when warm temperatures prevail (Berry and Taylor, 1968). Nighttime temperature inversions keep aphids aloft (Berry and Taylor, 1968). Aphids have been blown hundreds of miles over mountains and across seas at high altitudes (Johnson, 1957). Dickson and Laird (1959) observed populations of alates drifting over arid areas nearly 100 miles (about 150 km) from their breeding sites.

The principcal modes of aphid dispersal and migration were listed by Taylor (1965) as: (1) directed boundary layer flight, (2) stratiform drift, (3) cumuliform drift, and (4) jet stream transport. Visual cues orient alates upwind and determine their regulatory reactions to wind. Optomotor responses are most operative within the boundary layer (Kennedy and Thomas, 1974). The number of landings and re-take-offs is determined by the climate within the boundary layer and the suitability of host plants landed upon (Blackman, 1976).

The peak flight period for summer dispersal flights of Myzus persicae is July 25 through August 14 in New York (Tingey and van de Klashorst, 1976). Summer dispersal within the Flathead Valley of Montana is comparable. This emigration is a steady departure of a few individuals from secondary host plants from right before the peak density period until the end of the season (Blackman, 1976). Spatial patterns of flights are consistent from year to year within regions despite fluctuations in total numbers. And these distributions and their changes have more bearing on the control of the peach aphid than the number of dispersing aphids (Taylor, 1977).

Lewis (1970) observed insects being deposited by the wind leeward of a windbreak of tall trees. The deposition was enhanced by direct incident winds. Two to eight times the numbers of small bodied ($\underline{\underline{\bullet}}$2 mm^2 body area) insects were deposited to the leeward side of the break than to the windward side. He suggested that this deposition was due to the calm recirculation area leeward. Lewis and Dibley (1970) found that recirculation currents tended to move toware a barrier leeward near the ground and away from the barrier leeward near the shear layer. Insect deposition in the recirculation area by the wind depended upon gusts of wind blowing insects into and out of the area. Bowden and Dean (1977), however, found that the floristic diversity of the areas adjacent to windbreaks was predominantly responsible for the distribution of flying insects near to them.

APPENDIX F - Two Transmission Experiments with PLRV

In this appendix are given the data for two transmission experiments of potato leafroll virus in Russett potatoes transmitted to Physalis floridana Rydb. (ground-cherry) via apterous last instar nymphs and adults, and adult alate Myzus persicae. Both aphid morphs were taken from a single glasshouse clone reared on PLRV-infected Russett potatoes maintained at 15°C to 30°C in a glasshouse exposed to the prevailing autumn and winter photoperiods at Bozeman, Montana (45° 40'N Lat., 111° 00'W Long.). Indicator plants (P. floridana) were grown from seed in artificial soil (sand, peat, perlite; 1:1:1) in a growth chamber maintained at 20°C to 25°C daytime temperature and 17° to 20°C nighttime temperature. Air moisture in the chamber was kept at 70% to 85% relative humidity. Photoperiod was kept at 16 hours of light and 8 hours of total darkness for all indicator plants until transmission tests were completed, then the plants were removed to a glasshouse room to await symptom expression. Conditions of symptom expression were similar to those of the aphid colonies reared on potatoes. Symptoms were read according to those described by Kirkpatrick (1948).

For the first experiment (Table 9) apterous peach aphids were transferred to indicator plants at the 2-4 leaf stage of development in the growth chamber. Three transmission times, or inoculation feeding times of 15 minutes, 30 minutes and 60 minutes were used. For the

15-minute series transmission times were measured from the time each aphid's rostrum contacted a leaf until 15 minutes of continuous contact had elapsed, or until the time of contact between rostrum and leaf totaled 30 minutes. For the 30-minute and 60-minute transmission series, transmission times were measured for a 30 minute and a 60 minute continuous contact between rostrum and leaf, respectively, or until the contact times totaled 2 hours.

In the second experiment (Table 10), newly emerged winged peach aphids were caged on 2-4 leaf stage indicator plants (P. floridana) within the growth chamber for 24-hour intervals throughout their entire lives. Indicator plants were removed and replaced at 24-hour intervals. Removed plants were placed in a glasshouse for pLRV symptom expression. Inoculation feeding times for this experiment were not measured although all aphids were observed in feeding posture on plants during each 24-hour interval tested.

At $p = 0.01$ for experimental error, the observed transmission frequencies of 0.20, 0.44 and 0.36 for the 15-, 30- and 60-minute inoculation feeds, respectively, were not significantly different from the overall frequency of transmission of 0.33 for 75 trials. And at $p = 0.01$ for experimental error, the observed frequency of transmission for eighty 24-hour intervals of adult life for winged peach aphids was 0.44. This was not significantly different from the observed frequency of transmission occurring within the first seven 24-hour

Table 9. PLRV transmissivity by apterous *Myzus persicae* using inoculation feeding times of 15, 30 and 60 minutes.

	Inoculation Feeding Time			
	15 minutes	30 minutes	60 minutes	
# Indicator Plant Infections Per 25 Trials	5	11	9	
Transmission Frequency	0.20	0.44	0.36	Total - 25/75 = 0.33

Table 10. PLRV transmissivity by adult alate *Myzus persicae* throughout the aphid's life.

	I	II	III	IV	V	VI	VII	VIII	IX
# 24-hour Intervals In Life	16	12	1	20*	6	4	16	1	6
# Indicator Plant Infections Per 24-hour Intevals	4	7	0	8	3	2	9	0	2

Transmission frequency during first 7 intervals = 24/46 = 0.52

Transmission frequency during remaining intervals = 11/34 = 0.32

Transmission frequency during all intervals = 35/80 = 0.44

*Two of these interval readings were discarded due to the possibility of contamination.

intervals or the remaining 24-hour intervals of the aphids' lives. All infections occurred at random and were independent of one another.

The average longevity observed for adult alate Myzus persicae was 9.1 days. Nymph deposition by these adults occurred in more than half of the 24-hour intervals of the experiment.

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Aldrich, Daniel F
Overwintering, springtime development and migration of some Aphidae

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