ABSTRACT

Title of Thesis: The Life Cycles, Ecology, and Evolution of the Witch-hazel Leaf Gall Aphid, Hormaphis hamamelidis (Fitch) (Homoptera: Aphididae)

Carol Dean von Dohlen, Master of Science, 1987

Thesis directed by: Douglas E. Gill, Professor, Department of Zoology

Two divergent life cycles based on geographic location have been documented for the witch-hazel leaf gall aphid, Hormaphis hamamelidis (Fitch, 1851). At low elevations in northern Virginia, the aphid was found to have seven distinct generations alternating between the primary host, witch-hazel (Hamamelis virginiana L.), and a secondary host, river birch (Betula nigra L.). These findings confirm the original published life cycle description from the same locality. A second, abbreviated life cycle consisting of only three generations restricted to witch-hazel was discovered at high (1000 m) elevations in north central and northwestern Virginia. Aphids with each life cycle were sympatric at an intermediate elevation site. Based on available life cycle and geographic data, a preliminary phylogeny of the tribe Hormaphidini is proposed that suggests an unusual polarity in the evolution of aphid life cycles.

Several features of intraspecific interactions and host-plant relations were examined in both lowland and highland populations of Hormaphis. In contrast to previous publications documenting severe competition, density

effects, and habitat heterogeneity for another galling, host-alternating aphid, Pemphigus betae on Populus angustifolia, the effects of density and host-plant qualities on Hormaphis hamamelidis were fewer and more benign. Aphids did not compete for gall sites, and gall position and final leaf area did not influence reproduction. High gall densities negatively affected gall growth and aphid fecundity. Factors accounting for the differences in population dynamics between Hormaphis and Pemphigus are hypothesized and discussed.

THE LIFE CYCLES, ECOLOGY, AND EVOLUTION OF THE WITCH-HAZEL LEAF GALL APHID, HORMAPHIS HAMAMELIDIS (FITCH) (HOMOPTERA: APHIDIDAE)

by

Carol Dean von Dohlen

Thesis submitted to the Faculty of the Graduate School of the University of Maryland in partial fulfillment of the requirements for the degree of Master of Science
1987

Advisory Committee:

Professor Douglas E. Gill
Professor Gerald S. Wilkinson
Professor Robert F. Denno
Dr. Manya B. Stoetzel

ACKNOWLEDGMENTS

I thank D. Gill for inspiration, enthusiasm, and assistance throughout the study, and for careful, thoughtful review of the manuscript. I am grateful to M.B. Stoetzel for her continuing interest in the project, and for valuable suggestions, resources, and generous assistance in numerous aspects of the research. For identification of aphid predators, I thank R. J. Gagne' (Cecidomyiidae), R. D. Gordon (Coccinellidae), R.W. Hodges (Tortricidae), and F. C. Thompson (Syrphidae) of the Systematic Entomology Laboratory, U.S. Department of Agriculture, and O. S. Flint (Chrysopidae), Department of Entomology, Smithsonian Institution. I thank E. Perry and L. D. Smith for assistance with the data analysis. R. Denno kindly provided use of the leaf area meter. D. Gill, J. Heisler, and L. Coen gave assistance in the field. The Shenandoah National Park administration graciously permitted field work in the park. Computer facilities were supplied by the Computer Sciences Center of the University of Maryland. The work was funded in part by a grant-in-aid from the Sigma Xi Research Society and National Science Foundation grant DEB 01-5-24026. I am grateful to the members of the examining committee, D. E. Gill, M. B. Stoetzel, G. S. Wilkinson, and R. F. Denno, for their participation and many valuable comments.

TABLE OF CONTENTS

Chapter 1

Geographic variation and evolution in the life cycle of the witch-hazel leaf gall aphid, *Hormaphis hamamelidis*

List of Tables

List of Figures

INTRODUCTION

The diversity and complexity of life cycles within the family Aphididae present many challenging problems for systematists and developmental geneticists (Blackman, 1974; Dixon, 1985a; Eastop, 1973a). Different strains or host races within species may exhibit distinctive host preferences and color polymorphisms, (Dixon, 1985a,b; Eastop, 1973b); alate and apterous individuals, sexual and asexual morphs, and even defensive 'soldiers' (Aoki, 1977) may be found within a single aphid clone. Cyclical parthenogenesis (alternating asexual and sexual reproduction) is coupled both with polyphagy and monophagy, and host alternation and host specificity. However, some clones have persisted for years by continuous parthenogenetic reproduction without any sexual episodes (Dixon, 1985a,b; Blackman, 1974). Many aphid species vary in the number and timing of generations over the course of their reproductive season. Local environmental conditions such as temperature, photoperiod, host plant quality, and population density can play critical roles in the determination of alary (winged versus wingless) morphs (Dixon and Glen, 1971; Hille Ris Lambers, 1966; Johnson, 1965; Lees, 1966). The influence of photoperiod and temperature on the timing of sexual females and males is also well established (Blackman, 1975; Dixon, 1971; Kenten, 1955; Lees, 1959; MacGillivray and Anderson, 1964).

Defining or documenting reproductive isolation can be very difficult in groups with complete apomixis or extended parthenogenesis. The diversity of morphology and ecology among different populations within some aphid species calls into question the pertinence of the traditional "biological species" to this family (Shaposhnikov, 1981, 1984). In some cases, polymorphisms have been resolved to be distinct species (Blackman and Paterson, 1986), but in other species, designations have been made only on the basis of their different host plant preferences (Blackman, 1974). In still other cases, strains that exhibit clearly divergent host affinities have not been separable as species biochemically (Guldemond, in press).

Intraspecific variation with respect to the presence or absence of host alternation appears to be rare in aphids with holocyclic life cycles. Life cycle variation within species, whether or not geographically based, occurs almost exclusively as persistent anholocyclicity (incomplete cycles) within heteroecious species, i.e. asexual generations that remain on the secondary hosts year round (Markkula, 1963; MacGillivray, 1972; Blackman, 1972, 1974). Only a few possible cases of both heterocious and monoecious holocyclic strains within one species are at present known: small populations of Dysaphis reaumuri (Mordvilko) normally alternating from Pyrus to Galium stay on Galium throughout the summer, and Dysaphis plantaginea (Passerini) may contain populations that remain on Pyrus during the summer (Blackman

and Eastop, 1984). Both host-alternating clones and clones resident on the primary host were found in Cryptomyzus galeopsidis Oestland (Guldemond, in press). Alates of Myzus cerasi F. on the primary host colonized other parts of the same host, as well as secondary herbaceous hosts, and both monoecious and heteroecious life cycles apparently exist in Brachycaudus divaricatae Shap. and Dysaphis piri B.d.F. (Shaposhnikov, 1959).

Similarly, cases of both heteroecious species and species monoecious on the primary host within the same aphid genus is unusual, although rare examples may be cited: Eriosoma lanigerum migrates from elm to apple, but E. rileyi remains on elm (Davidson, 1927a,b); Pemphigus bursarius Oestland migrates from Populus to roots of herbaceous plants, while P. spirotheca remains on Populus (Davidson 1927a,b). Aphis evonymus F. is distinguished from the otherwise heteroecious Aphis fabae group by its restriction to the primary host Evonymus (Müller, 1985).

Because the majority of species in the Aphididae are monoecious and only 10% of species are host-alternating, the polarity of evolution in life cycles for the aphid family as a whole is presumably monoecy to heteroecy, i.e. through the acquisition of one or more secondary summer hosts (Eastop, 1973a). Mordvilko (1928, 1935b) considered heteroecy an endpoint in evolution, but Kennedy and Stroyan (1959) and Eastop (1973a,b) review cases where monoecy clearly is secondarily derived from heteroecy (by the secondary loss of

the summer host). Many host-alternating aphids do have close monoecious relatives that complete their life cycles on the secondary host(s) (usually a summer annual) of the heteroecious species (Hille Ris Lambers, 1950, 1979; Blackman and Eastop, 1984). Loss of the primary host and adaptation of the sexual generation to the secondary host, or strictly parthenogenetic propagation on the secondary host has been a frequent event in aphid evolution (Blackman and Eastop, 1984). Interestingly, such cases illustrating secondary losses of heteroecy to date include only species that have converted to monoecious life-styles (anholoclic and holocyclic) on former secondary hosts. There appear to be no examples of secondary reversion from heteroecy to monoecy on the primary host; indeed, that scenario would be difficult to reconstruct and substantiate phylogenetically.

The specific case of Hormaphis hamamelidis on witch-hazel, Hamamelis virginiana in North America is unusual, not only in its life history variation, but also in its use of a woody summer host when most heteroecious aphids migrate to nutritious annual species. The first to describe the complex life cycle of Hormaphis hamamelidis (Fitch 1851) from the Potomac River Valley, Pergande (1901) found that the aphid had 7 distinct generations alternating between witch-hazel (the primary spring and fall host) and river birch, Betula nigra (the secondary summer host). Fundatrices (generation I) hatched from overwintering eggs before bud break in early spring and established galls on

the developing leaves as they unfolded. Parthenogenetic alate individuals of the second generation (II) emerged from galls in late spring and flew to leaves of river birch to deposit larvae of the first summer generation (III). Apterous, aleurodiform generations III-V (superficially resembling Aleurodidae in body outline and waxy secretions) proliferated on birch leaves through the summer; larvae of the alate generation VI (sexuparous fall migrants) matured on birch in September and returned to leaves of witch-hazel to deposit females and males of the wingless sexual generation (VII). Males and females (oviparae) mated and the females each produced 5-10 overwintering eggs.

Several years after Pergande's (1901) observations, Morgan and Shull (1910) recognized an abbreviated, possibly monoecious population of witch-hazel gall aphids at Cold Spring Harbor, New York. They observed alates emerging from galls and producing sexuales directly on witch-hazel leaves. These alates rejected birch leaves (Betula lenta and B. lutea) when offered for larviposition sites. Morgan and Shull (1910) did not offer either river birch (B. nigra), the normal secondary host of H. hamamelidis or paper birch (B. papyrifera), because neither of those birch species was found in the vicinity of the study site. Microscopic dissection of adult and immature alates within galls revealed sexual embryos. Morgan and Shull (1910) concluded that birch was not an obligate secondary host in the life cycle of H. hamamelidis in their locality, and suggested

that embryos from gall alates at Pergande's study site should be examined microscopically to confirm their reproductive morphology.

Reviewing Pergande's (1901) and Morgan and Shull's (1910) work, Morkvilko (1930a, 1935a) speculated that perhaps Hormaphis galls opening early in the season produce parthenogenetic emigrants that fly to birch, and galls developing later produce sexuparae (forms bearing the sexual generation) that remain on witch-hazel. He also asserted that spring migrants of H. hamamelidis fly to B. spinosa and B. papyraceae. Lampel (1968) conjectured that a 2-yr life cycle similar to that of Hamamelistes spinosus (also heteroecious on witch-hazel and river birch), in which coccidiform larvae overwinter on birch, might also exist in Hormaphis hamamelidis.

Mordvilko (1930a, 1935a) and Lampel (1968) cite Morgan and Shull's (1910) work as evidence of a monoecious complete life cycle in the genus Hormaphis. Börner (1952) declared the monoecious form of H. hamamelidis a new species, H. shulliana, but did not include a proper taxonomic description. Eastop and Hille Ris Lambers (1976) recognized four valid species in the genus Hormaphis, but excluded H. shulliana Börner, 1952, which they considered a nomen nudum.

In his recent review of the phylogeny and taxonomy of the Hormaphidinae, Ghosh (1985) agreed with Eastop and Hille Ris Lambers (1976) and classified the tribe Hormaphidini into six definite species within the two genera Hormaphis

(four species) and Hamamelistes (two species). Admitting that the number of species was taxonomically difficult and the status of another six species was in doubt, Ghosh (1985) nevertheless asserted that the members of both genera had either complete life cycles alternating between Hamamelis and Betula, or were restricted to Betula.

In a paper that apparently has been overlooked in reviews of the Hormaphidini, Lewis and Walton (1958) studied the cytology of gall formation in H. hamamelidis at Mountain Lake, 1200 m elevation in the Blue Ridge Mountains in southwestern Virginia. They noted that the aphids there had an abbreviated, three-generational life cycle confined to witch-hazel. In contrast, H. hamamelidis at a low elevation site farther east in Danville, Virginia appeared to follow the host-alternating cycle described by Pergande (1901). The secondary host, B. nigra, grew at Danville, but did not occur at Mountain Lake. The differences in the life cycles of H. hamamelidis at the two locations were attributed to the shorter (by two months) growing season at Mountain Lake. Lewis and Walton's (1958) observations at Mountain Lake were consistent with the description of H. hamamelidis in New York by Morgan and Shull (1910), but unfortunately they did not publish quantitative details of the life cycles.

Clearly, the life cycle of Hormaphis hamamelidis is unresolved, and its taxonomic status as one species may be in question. The purpose of the present study was to conduct a comparative, quantitative investigation into the

life cycle of H. hamamelidis at four locations: a low elevation situation very close to the site of Pergande's (1901) original studies, two high elevation sites similar to where Lewis and Walton (1958) made their observations, and a mid elevation location where the two forms might be sympatric. Our simultaneous observations, collections, and ongoing experiments at these sites shed light on the striking life cycle variation in H. hamamelidis.

METHODS

Description of Field Sites

Observations and experiments were carried out at four sites: one lowland site, P, two highland locations, G and S, and one site at intermediate elevation, L. The lowland site P was at sea level along the Potomac River in the Dranesville District Park, Dranesville, Virginia. The dominant canopy trees at site P were hemlock (*Tsuga canadensis*), and sycamore (*Platanus occidentalis*) along the stream banks, and tulip poplar (*Liriodendron tulipifera*) and white oak (*Quercus albus*) on the drier knolls. Witch-hazel, mountain laurel (*Kalmia latifolia*), dogwood (*Cornus florida*), and young black birch (*Betula lenta*) were common in the understory. Several young river birch (*B. lenta*) grew at the immediate experimental site, but many full-grown specimens lined both east and west banks of the Potomac as close as 0.5 km. Site G was 1000 m elevation in the Shenandoah Mountains (George Washington National Forest) in western Virginia. Also at 1000 m, Site S was in the Blue Ridge Mountains (Shenandoah National Park, Central Section) in central Virginia. Both highland sites had the characteristic vegetation of the western mid-Atlantic valley and ridge physiographic region: chestnut oak (*Quercus prinus*) and white oak were dominant trees on the dry ridges, while basswood (*Tilia americana*), tulip poplar, and yellow birch (*Betula alleghaniensis*) were common species along the moist stream beds. Witch-hazel and mountain laurel were the

principal understory shrubs. The intermediate elevation site L was at 183 m in the Piedmont Plateau in the Little Bennett Regional Park, Clarksburg, Maryland. The vegetation at site L was very similar to site P except that stands of river birch were not known to be nearer than several kilometers to the south.

Analysis of Gall Contents

To monitor the development of aphid generations I and II in galls, samples of witch-hazel leaves with single Hormaphis galls were collected weekly at site P from May to June, 1985 and from April to June, 1986. Galls were collected weekly at sites G and S from May to October in 1985, and from April to October in 1986. At site L, galled leaves were gathered weekly or biweekly from June to October, 1985 and from April to October, 1986. At locations P and G, samples consisted of 5 leaves with galls from all parts of each of 6 tagged witch-hazel shrubs (individual genets), totalling 30 per week per site. At site S, weekly samples consisted of 5 leaves from each of 6 shrubs in 1985, and and in 1986 from 3 shrubs per week early in the season, and 3 additional shrubs in later weeks. At site L, due to the overall scarcity of galls in 1985 and 1986, and an invasion of gypsy moths, Lymantria dispar in 1986, galls were collected haphzardly from more than 10 different shrubs throughout the season. Leaves were transported to the laboratory in coolers with ice and stored in a refrigerator

at 5oC. Analysis of samples was completed within 24-48 hr of collection.

Gall size was determined by measuring with calipers: height from tip (above upper leaf surface) to base (lowest point below leaf underside), and width at widest girth above upper leaf surface. Each gall was split lengthwise and the residents (generation I fundatrix and her parthenogenetic generation II progeny) were gently transferred with a paintbrush to filter paper and counted under 80x with a Wild dissecting microscope. Any non-aphid gall inhabitants or predators were noted and retained for identification.

At site L, 2 bushes on which aphids had been present in 1985 were tagged in 1986 for nondestructive monitors of the early spring hatching and gall development. All galls developing on the 2 bushes were numbered and their heights were measured weekly from mid May to mid July. Galls were inspected individually each week for evidence of emerging mature alates.

Aleurodiform Generations III-V and Fall Alate Generation VI on River Birch

In order to follow the development of Hormaphis summer generations on river birch, 3 replicate branches (on separate trees) with 12-20 leaves each were tagged for repeated observations. Weekly counts were made through a magnifying lens of immature instars and adults of the aleurodiform generations (the three generations described by

Pergande (1901) were not morphologically separable in the field) and immature and adult alate generation VI.

Two Betula species, black birch and yellow birch, were present at the highland sites G and S, and black birch was found at sites P and L. These species and other related members of the Betulaceae (Alnus, Carpinus) were inspected closely for the aphid summer generations.

In 1986 after the spring migration to birch at site P, selected birch leaves with aphids were monitored closely in order to confirm the number of aleurodiform generations. A small branch of 10 river birch leaves was treated at its base with TanglefootR (a sticky resinous material) to prevent immigration of the mobile 1st instars. As soon as galls had emptied in late June and no more spring alates were observed on birch, all aphids except 1st and 2nd instar generation III were removed with a paintbrush from the experimental leaves. The young cohort of aphids was allowed to mature. As soon as the majority had reached maturity, all immature larvae were again removed. The following week, after adult III had borne substantial numbers of generation IV larvae, all adult III were removed. This technique of allowing larval development to maturity, removal of lingering larvae, followed by adult removal after further reproduction, synchronized development and eliminated overlap of generations that were otherwise indistinguishable in the field. The process was repeated until the

morphologically distinct offspring of generation VI (fall migrants) were produced.

Sexual Generation on Witch-hazel

At site P when the first fall migrants (sexuparous generation VI from river birch) appeared on witch-hazel in early September to bear the sexual generation, 5 leaves per each original sample bush (total=30) were gathered weekly and examined at 80x under a Wild dissecting microscope in the laboratory. Numbers per leaf of immature live, dead, and mature oviparae and males were counted; predators were noted and samples collected for identification.

To follow the development of sexuales at sites G, S, and L, the undersurfaces of witch-hazel leaves (the same leaves used in the studies of generation I and II) were examined and aphids counted in the laboratory as described above. At site L, fall migrants also appeared on several witch-hazel bushes in September and produced a "late" cohort of sexuales. Therefore, in addition to the regular samples of galled leaves taken at site L to monitor the progress of the "early" cohort of sexuales born in July, 5 leaves per bush were collected from each of 4 bushes where migrants had deposited the "late" sexual generation.

Dispersal of Highland Alate Generation II

As it became clear that highland generation II alates were not migrating to secondary hosts in the highlands,

monitors were conducted within bushes and among bushes to determine the extent to which alates were colonizing new primary host plants. To assess the colonization of ungalled leaves within a galled bush (i.e., to see whether alates moved off their natal leaves in substantial numbers) weekly samples of 5 ungalled leaves per each of the 6 original sample bushes were collected. Immature live, dead, and adult oviparae and males were counted in the laboratory under 80x. To determine whether highland alates were flying from their natal bushes to other witch-hazel bushes, 5 leaves were collected from each of 6 completely uninfested bushes at sites G and S in 1985, and sexuales counted as described above.

Experimental Test of Host Preference by Alate Generation II

In early September, 1985, when highland alates were still emerging from galls, the host-plant specificity of these alates was tested on live bushes in the field and in the laboratory. In the field, 5 alates were extracted from highland galls and placed on leaf undersurfaces of 5 out of 10 leaves which were then enclosed in a Nytex nylon bag. Two replicates each on witch-hazel (controls), black birch, and yellow birch were set up *in situ*. In addition, 2 replicate bags were arranged on potted river birch in the laboratory. After 2 weeks, the bags were removed and the leaves examined for larvae.

In 1986, the host preference of mature alates emerging from lowland galls was tested in the laboratory. Fresh leaves of both witch-hazel and river birch, and galls containing mature alates were collected at site P in early June and transported on ice to the laboratory. Choice chambers were constructed of 300 ml glass jars covered with fine nylon mesh. Into each was placed 2 test leaves, 1 witch-hazel leaf and 1 river birch leaf, propped upright in squares of moist OasisR (a water-absorbant medium used in flower arrangements). One alate was introduced into each chamber and left for 48 hr or until death. OasisR was re-moistened if necessary. At the end of the experiment both leaves were examined closely for larvae, and larval morphology (sexual or asexual aleurodiform) was recorded.

Experimental Cross-Mating of Lowland and Highland Sexuales

In late September 1986 when both lowland and highland sexual females and males were mature in the field, leaves bearing adults were collected from sites P and G and transported in a cooler with ice to the laboratory. Aphids were kept cool and immobile in a refrigerator until removal from the leaves for experimentation, within 48 hr of collection. Four pairings were performed, 2 experimental (lowland female x highland male, highland female x lowland male) and 2 controls (lowland female x lowland male, highland female x highland male). For all pairings except the highland control, either 1 female and 2 males, or 2

females and 4 males were removed from a leaf and placed into an 11 dram glass screwtop test-tube, which contained a short length of freshly cut witch-hazel twig. In the highland control pairing, 1 female and 2 males were placed into each test tube. In addition to the other tubes, 1 test tube for each pairing type was prepared with 8-10 females and 20-25 males. All twigs were examined carefully prior to the experiment under 80x and any contaminant eggs were removed. Aphids were observed for 20 minutes, then left for 48 hr or until the female had expired. Twigs were removed and the newly laid eggs were counted under 80x.

RESULTS

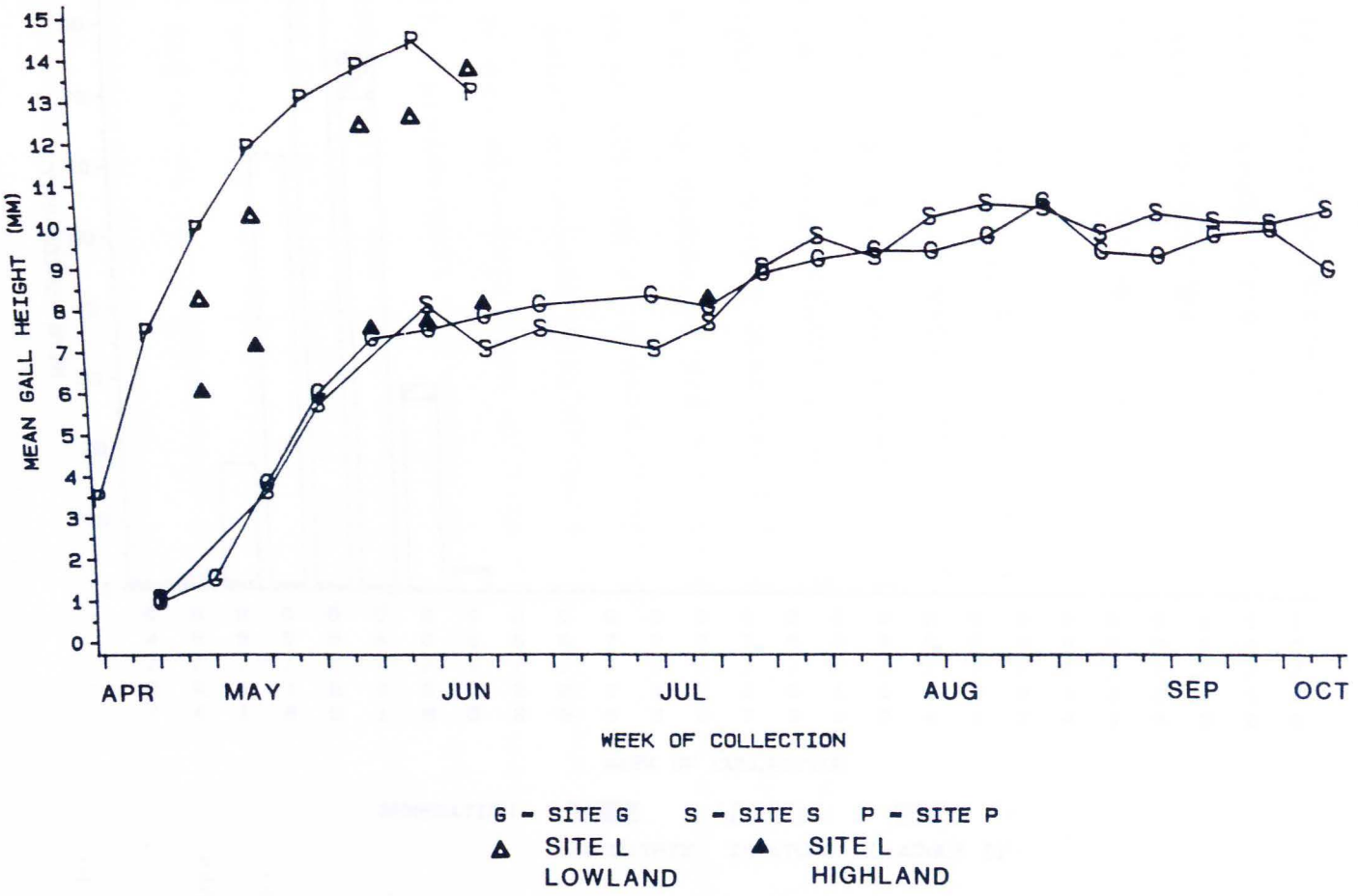
The results for both sample years (1985 and 1986) were consistent with regard to the development and timing of aphid generations. All figures depict data collected in 1986 unless otherwise noted.

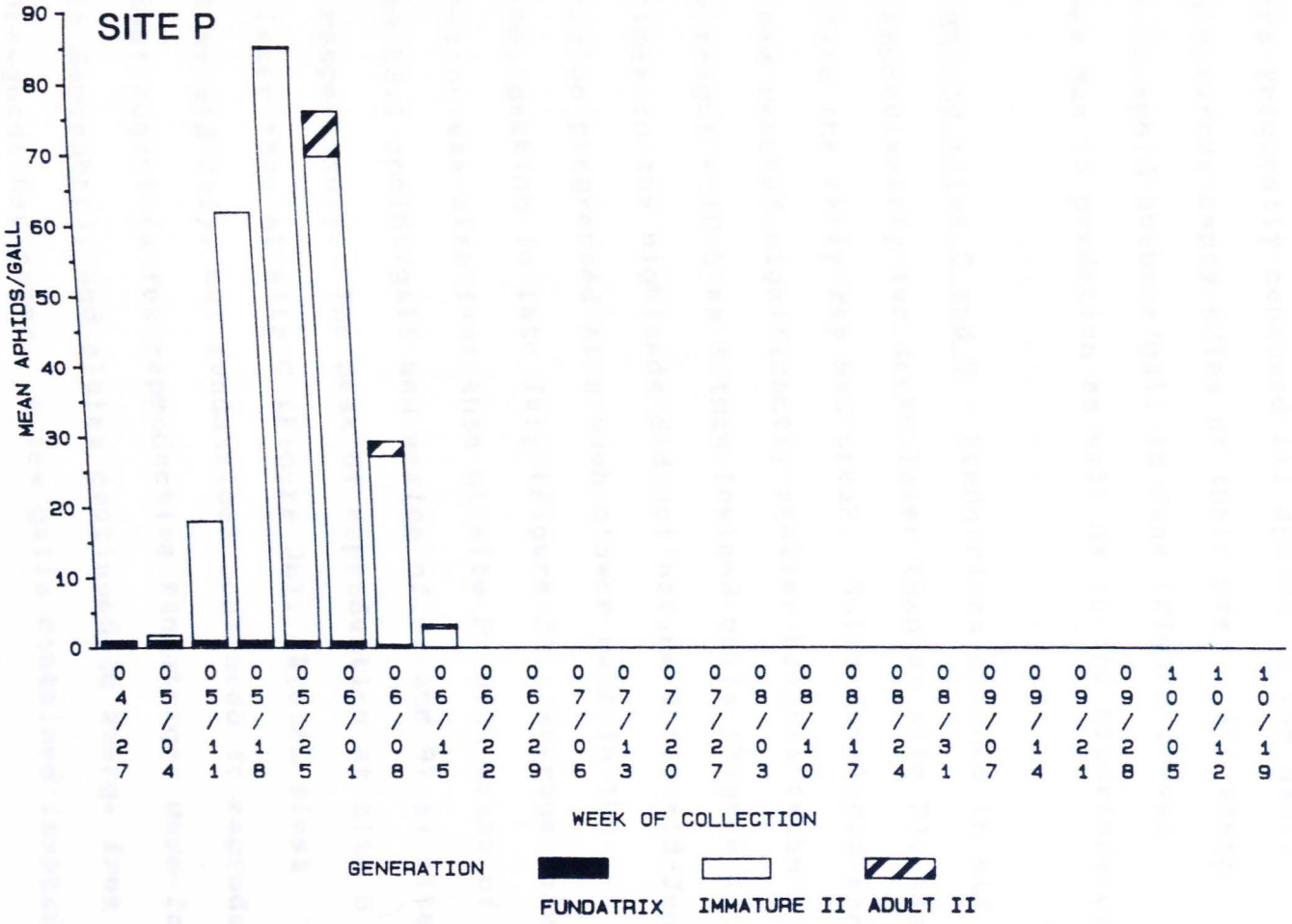
Gall Generations I and II on Witch-hazel

Lowland site P - The development of the aphid generations I and II in galls at site P confirmed Pergande's (1901) observations: generation I fundatrices hatched at the end of March and crawled to the unopened leaf buds. After settling on the buds aphids did not appear to shift position or feed for 1-2 weeks; they remained in the first instar until bud break in mid April. As a leaf expanded the juvenile fundatrices probed the leaf undersurface with their probosces and initiated gall growth around themselves. Cone-shaped pouch galls developed rapidly on the expanding leaves to a mean maximum height of 14.5 mm by early June (Figure 1). However, fundatrices reached maturity and began to reproduce by the first week of May (Figure 2). At peak reproduction, mean aphids/gall was 85.2, with a maximum of 149. Generation II developed through 4 larval instars and the mature alates began to depart from galls through the ventral opening by the end of May; all galls were empty by late June (Figure 2). By mid June close to 70% of galls sampled contained a predator, either the larva of a coccinellid beetle (Scymnus festatus) (60% of galls) or a

Figure 1. Weekly mean heights of Hormaphis hamamelidis galls on witch-hazel collected at lowland site P and highland sites G and S, and gall heights measured in situ at intermediate elevation site L. Lowland galls were significantly taller at peak height than highland galls (analysis of variance, error df=42, F=16.82, p<.0001).

Figure 2. Weekly mean numbers per gall of lowland generation I (fundatrix) and alate generation II (spring migrants) aphids on witch-hazel at site P.


MEAN GALL HEIGHT (MM)
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
APR
MAY
JUN
JUL
AUG
SEP
OCT
WEEK OF COLLECTION
G - SITE G
S - SITE S
P - SITE P
SITE L LOWLAND
SITE L HIGHLAND


SITE P
MEAN APHIDS/GALL
90
80
70
60
50
40
30
20
10
0
04/27
05/04
05/11
05/18
05/25
06/01
06/08
06/15
06/22
06/29
07/06
07/13
07/20
07/27
08/03
08/10
08/17
08/24
08/31
09/07
09/14
09/21
09/28
10/05
10/12
10/19
WEEK OF COLLECTION
GENERATION
FUNDATRIX
IMMATURE II
ADULT II

syrphid larva (Syrphidae) (13%); the two predators were occasionally found together in the same gall. These large predators frequently consumed all aphids in the gall, leaving numerous empty skins of their prey. The steep decline in aphid numbers/gall in June (Figure 2) was therefore due to predation as well as to the departure of alates.

Highland sites G and S - Fundatrices hatched in mid April (approximately two weeks later than at site P), again well before the early May bud break. Galls developed more slowly and reached significantly smaller heights (mean maximum height = 10.6 mm) than lowland galls (Figure 1). Fundatrices in the highlands did not mature until mid-June. Reproduction progressed at a much slower rate in the mountains, peaking in late July (Figure 3). Average peak reproduction was also less than at site P, with means of 55.4 and 53.1 aphids/gall and maxima of 91 and 97 at sites G and S, respectively. The peak of reproduction at site S was 1 week later than at site G (Figure 3b). Alates first matured by mid-July, but fundatrices continued to reproduce throughout August (a few reproductive fundatrices were found in early September), and alates continued to emerge from July throughout September. A few galls contained immature and adult alates even at leaf drop in early October. Highland galls were not attacked by coccinellid larvae, and only rarely by syrphid larvae. However, several galls were invaded by lepidopteran larvae (Tortricidae) that burrowed

into the galls and fed on the inner walls. Aphids in these galls were eventually killed; whether death ocurred by starvation, predation, or by smothering in the large quantities of frass produced by the lepidopteran could not be determined. Accurate percentages of predation by tortricids could not be evaluated because these galls were systematically avoided during the collection of samples for life cycle data.

Intermediate elevation site L - Fundatrices hatched at site L by the second week of April; bud break commenced in the last week of April. It was immediately apparent that the monitor bushes harbored both "highland" forms and "lowland" forms of aphids: 45 out of 70 galls developed rapidly and produced mature alates in June; 25 galls developed slowly and their alates did not emerge until late July. The "lowland" type galls grew quickly to a large size (mean maximum height=13.9 mm) equivalent to galls as site P; "highland" type galls grew more slowly to smaller size (mean maximum height=8.1 mm) equivalent to the size of galls at sites G and S (Figure 1). The regular haphazard gall samples from tagged bushes at this site showed a bimodal distribution of reproduction consistent with the monitor bushes (Figure 4). The 4-wk hiatus in samples from late June to early July (Figure 4) was due to the extremely low numbers of "highland" forms: by the time "lowland" galls had emptied of aphids, all "highland" galls had been collected at the original site. Bushes in a second area at

the same site (discovered in July) harbored enough "highland" galls to sample for the remainder of the season. Galls of both types at site L also experienced predation or invasion by the coccinellid Scymnus festatus , syrphid larvae, and tortricid larvae.

Generations III - VI on River Birch

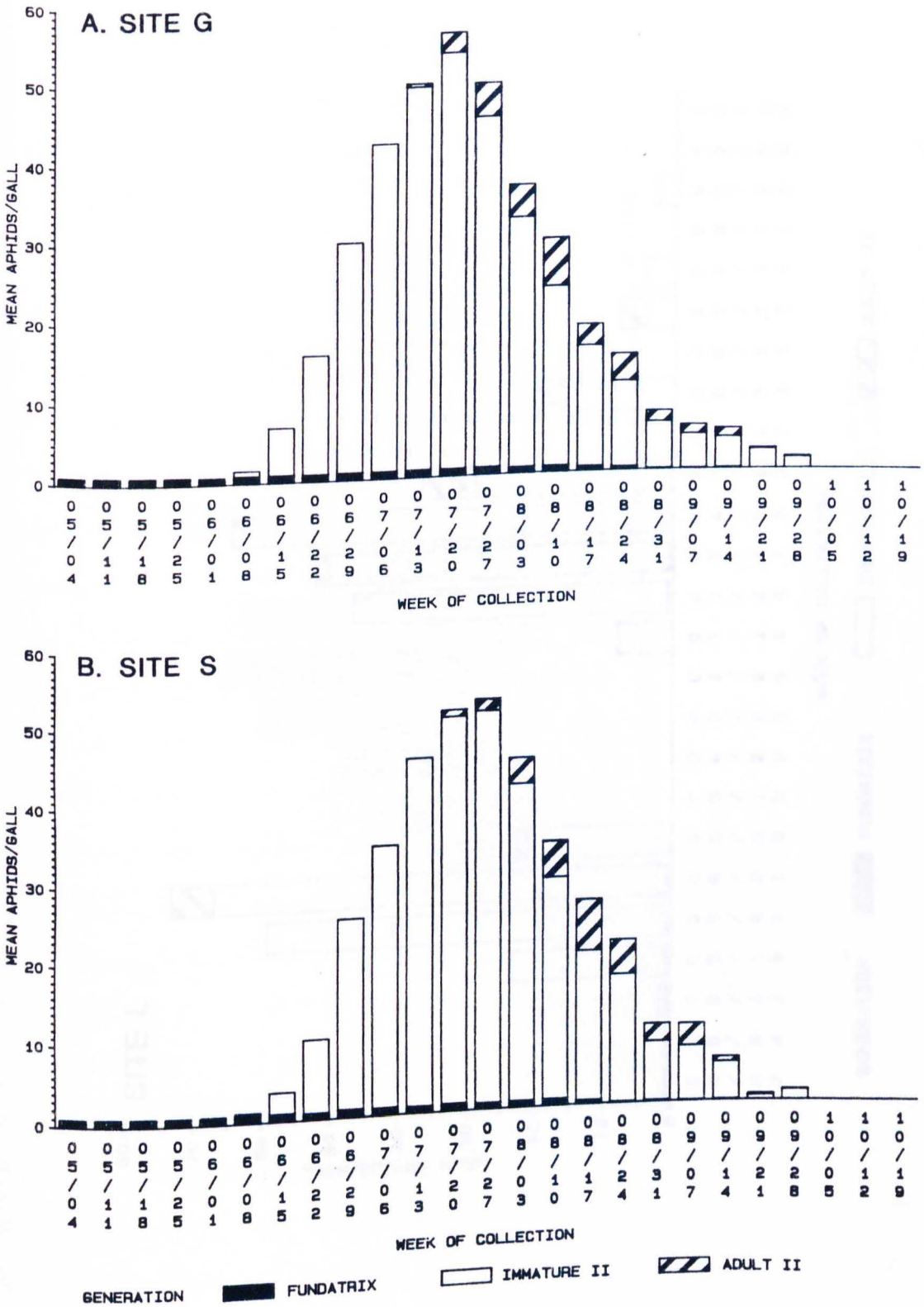
Site P - Shortly after alates began to emigrate from galls at site P, alates of identical appearance were observed on the undersurfaces of river birch leaves. Witch-hazel and river birch occurred in close proximity only at this site. The migrants produced numerous larvae of apterous, aleurodiform generation III on the birch leaves; aleurodiform aphids proliferated on birch throughout the summer (Figure 5). Larvae of alate (fall migrant) generation VI were first observed in early August and began to mature by early September (Figure 5). Counts after August 31 were from one monitor branch only, because all leaves on the 2 most heavily infested branches senesced and fell prematurely in August. Monitors of the branch where larvae and adults were removed sequentially confirmed that there were 3 aleurodiform generations. Many aphids on birch were consumed by syrphid, cecidomyiid (Cecidomyiidae), and neuropteran (Chrysopidae) larvae.

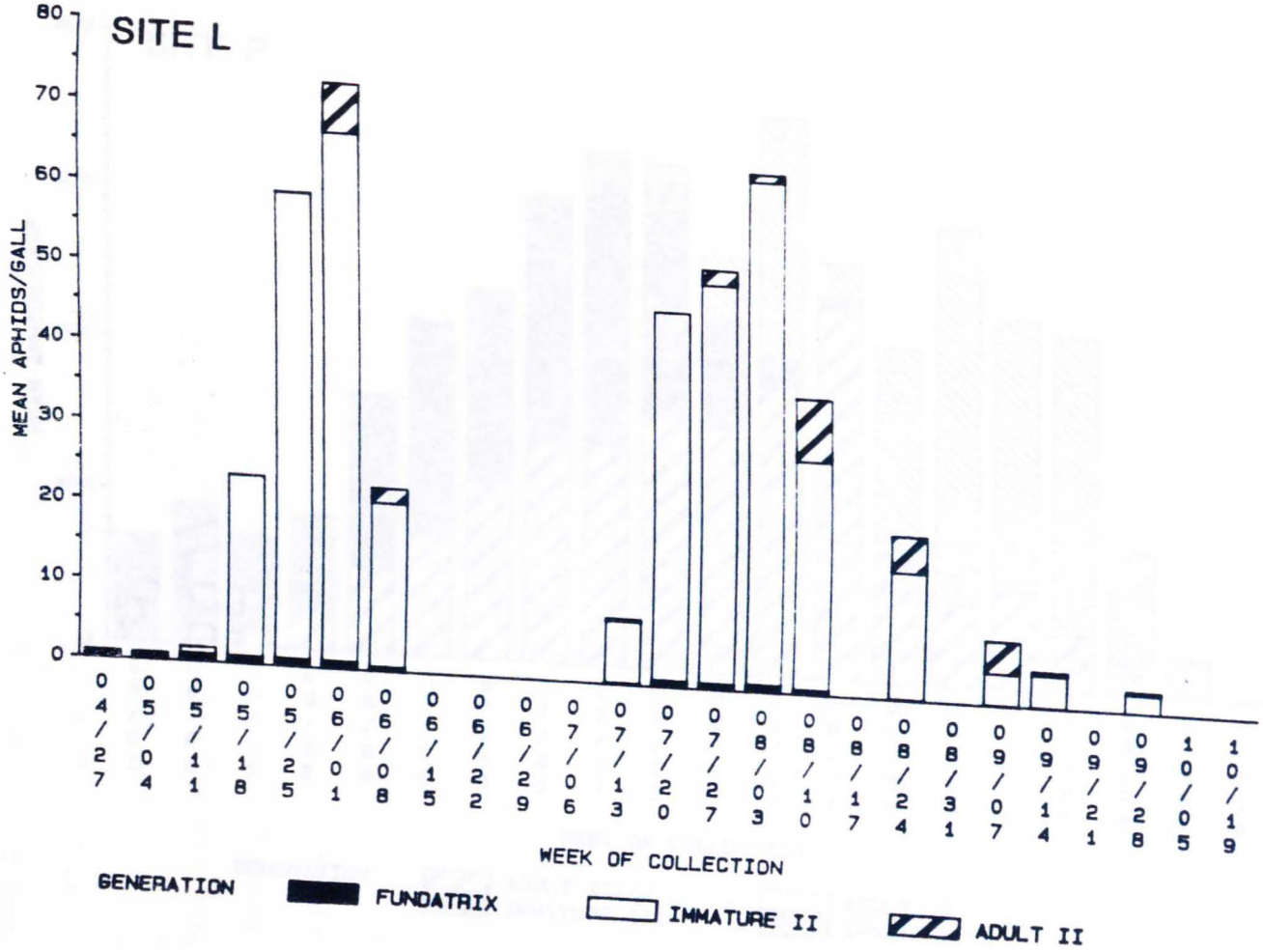
Sites G, S, and L - River birch, a lowland riparian species, was never found at the two highland sites G and S or at site L. Although both black birch and yellow birch at

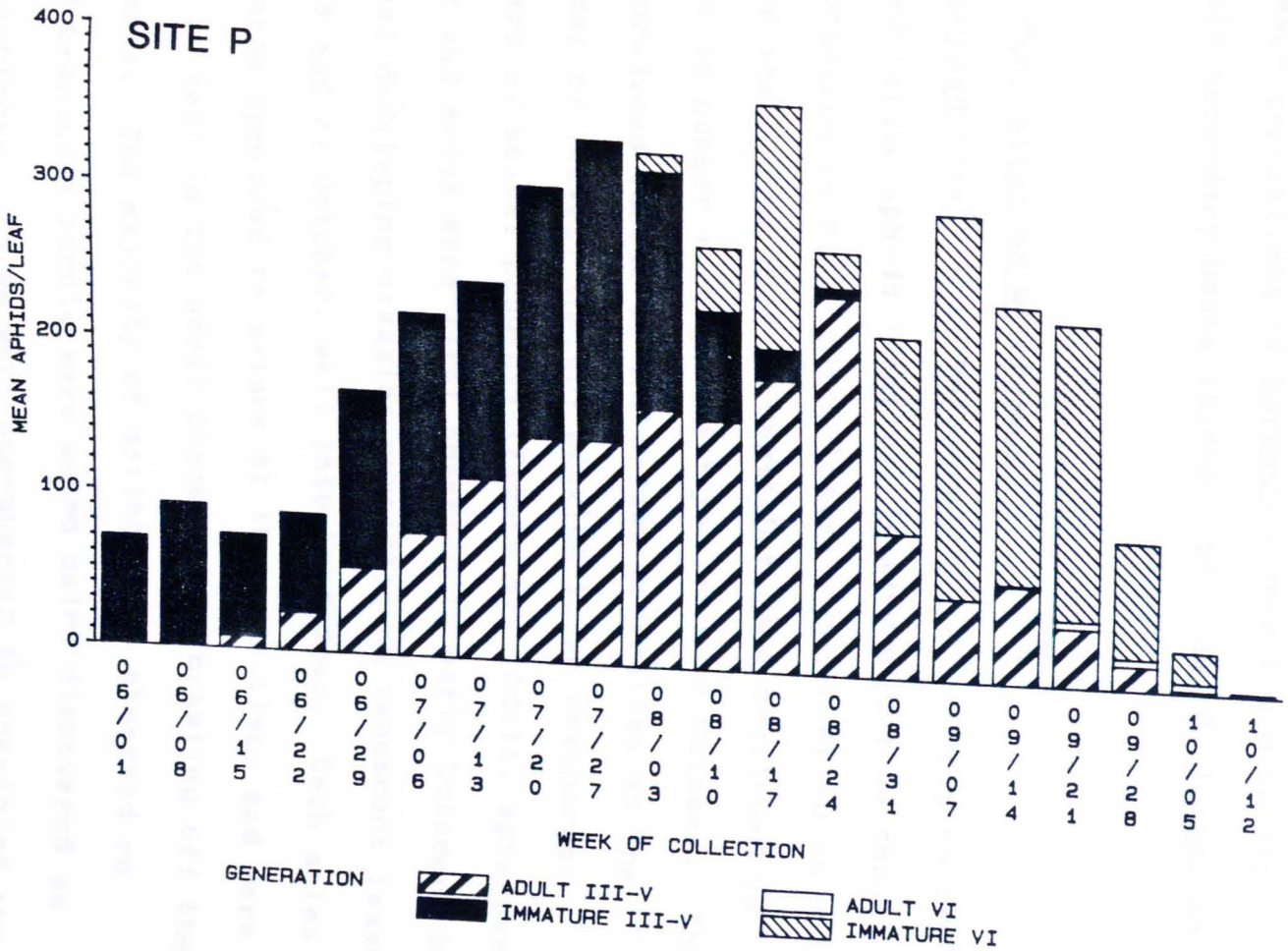
Figure 3. Weekly mean numbers per gall of highland generation I (fundatrix) and alate generation II aphids on witch-hazel. A. site G, B. site S.

Figure 4. Weekly mean numbers per gall of generation I (fundatrix) and alate generation II aphids on witch-hazel at intermediate elevation site L.

Figure 5. Weekly mean numbers per leaf of lowland summer apterous generations III-V and alate generation VI (fall migrants) on river birch at site P.


A. SITE G
MEAN APHIDS/GALL
0
10
20
30
40
50
60
05/04
05/11
05/18
05/25
06/01
06/08
06/15
06/22
06/29
07/06
07/13
07/20
07/27
08/03
08/10
08/17
08/24
08/31
09/07
09/14
09/21
09/28
10/05
10/12
10/19
WEEK OF COLLECTION
B. SITE S
MEAN APHIDS/GALL
0
10
20
30
40
50
60
05/04
05/11
05/18
05/25
06/01
06/08
06/15
06/22
06/29
07/06
07/13
07/20
07/27
08/03
08/10
08/17
08/24
08/31
09/07
09/14
09/21
09/28
10/05
10/12
10/19
WEEK OF COLLECTION
GENERATION
FUNDATRIX
IMMATURE II
ADULT II


SITE L
MEAN APHIDS/GALL
80
70
60
50
40
30
20
10
0
04/27
05/04
05/11
05/18
05/25
06/01
06/08
06/15
06/22
06/29
07/06
07/13
07/20
07/27
08/03
08/10
08/17
08/24
08/31
09/07
09/14
09/21
09/28
10/05
10/19
WEEK OF COLLECTION
GENERATION
FUNDATRIX
IMMATURE II
ADULT II


SITE P
MEAN APHIDS/LEAF
400
300
200
100
0
06/01
06/08
06/15
06/22
06/29
07/06
07/13
07/20
07/27
08/03
08/10
08/17
08/24
08/31
09/07
09/14
09/21
09/28
10/05
10/12
WEEK OF COLLECTION
GENERATION
ADULT III-V
IMMATURE III-V
ADULT VI
IMMATURE VI

G and S were examined closely for Hormaphis, no aphids were ever found on these potential secondary hosts. Similarly, no summer generations of Hormaphis were found on the possible secondary hosts (Alnus, Carpinus, B. lenta) at site L.

Sexual Generation on Witch-hazel

Lowland Site P - As Pergande (1901) had originally observed, alate aphids identical in appearance to those being produced on river birch leaves were observed on witch-hazel in the second week of September, and continued to increase in number through the first week of October. These alates produced larvae of the sexual generation on the undersides of leaves, thereby proving to be sexuparous (producers of sexual progeny) (Figure 6). Adult, apterous oviparae and males were first observed in early October, but the latest developing sexuales persisted on senescent leaves until the end of October, well into leaf drop. Both males and oviparae appeared to mature at the same time, and were observed to feed in the adult stage before crawling off the leaf to mate. The majority of matings were observed on twigs and branches; rarely were mated pairs discovered on the leaf surfaces. Males were one-quarter to one-third the size of females, moved actively, and in the laboratory were polygamous. Oviparae laid eggs in crevices of bark, often at a great distance from their natal leaf; they seemed to prefer the rougher bark of older, thicker branches and even

traveled to the main trunk for oviposition sites. Immature sexuales were preyed upon by larvae of both syrphid and cecidomyiid flies (Figure 6).

Highland sites G and S - The reason why no aleurodiform generations III-V, and alate VI (normally associated with river birch in the lowlands) were observed on any secondary host plants at the highland sites was because alates emerging from galls in late July immediately produced larvae of the sexual generation on their natal or adjacent leaves (Figure 7). Whereas lowland gall alates had been virginoparous (producers of asexual progeny) and migratory, highland gall alates proved to be sexuparous and nonmigratory. Highland alates at site G moved primarily within their natal bushes for larviposition sites: numbers of sexuales were not significantly different between galled and adjacent ungalled leaves (Student's t-test, $0.24 < p < 0.99$ for all 4 weeks analyzed over peak abundance; leaf areas did not differ significantly between galled and ungalled leaves by Student's t-test, $0.37 < p < 0.82$). However, alates were rarely found on uninfested bushes at the same site, and the numbers of sexual larvae on these bushes were significantly fewer than on infested bushes (Student's t-test $p << .001$ in each of 3 weeks analyzed).

The apterous sexual females and males matured in approximately 5 weeks; the first adults were observed in late August at both G and S (Figures 7). Adult feeding, ambulation off leaves to twigs, mating and egg-laying were

similar to those activities at lowland site P. Immature sexuales in the highlands were also preyed upon by the larvae of syrphid and cecidomyiid flies (Figure 7).

Intermediate Site L - First instars of the "early" cohort of sexuales were observed in late July and developed by the same chronology as site G and S sexuales, although their numbers were far fewer (Figure 8). The second set of alates that appeared on witch-hazels in early September was most noticable on several bushes where they had been abundant in 1985. The "late" cohort of sexuales produced by these alates developed in the manner of site P aphids (Figure 8). Both syrphid and cecidomiid larvae attacked immature sexuales at site L (Figure 8).

Alate Leaf Choice

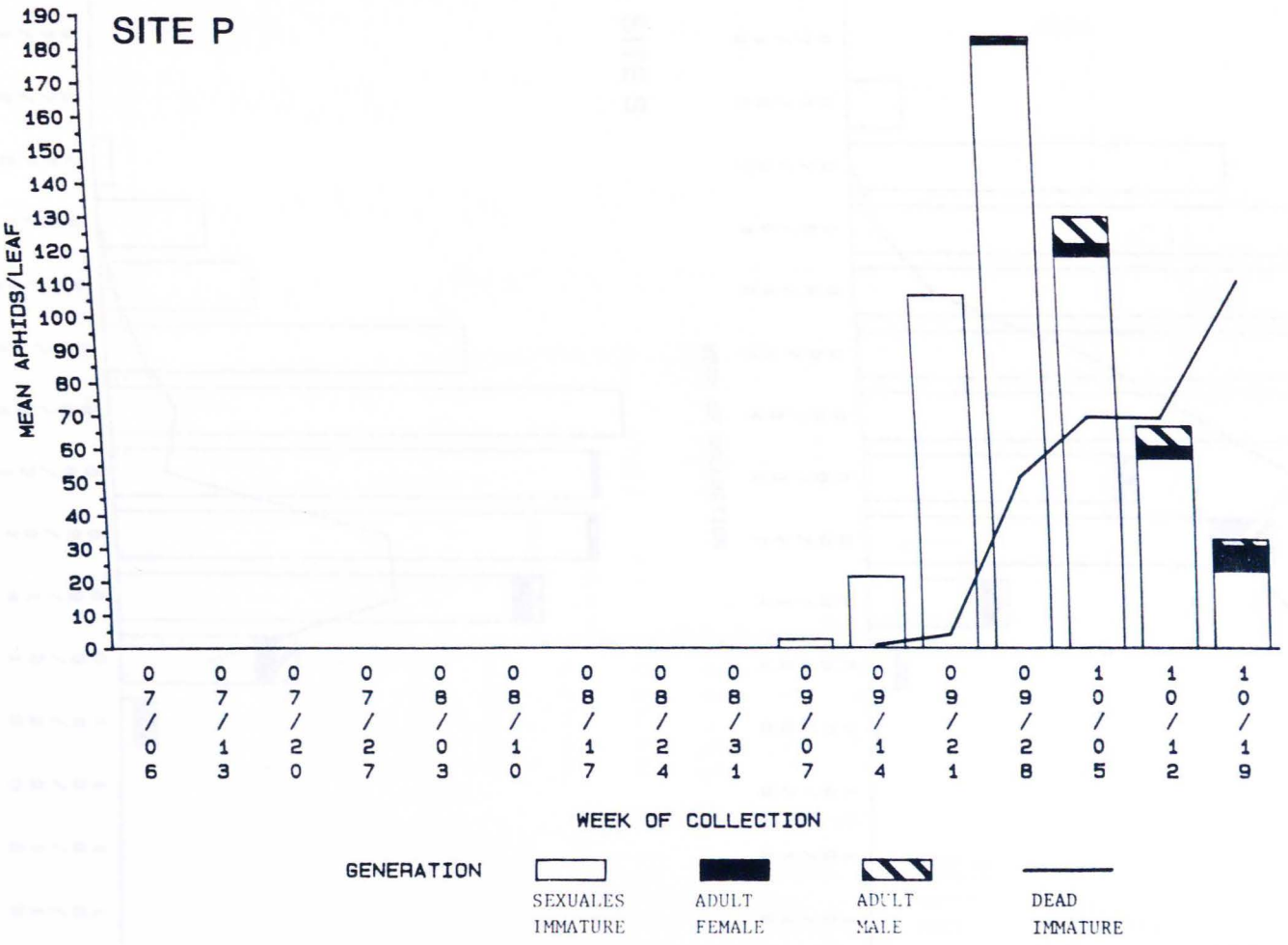
No offspring from highland alates were found on either black birch or yellow birch leaves in experimental bags in the field, or on river birch in the laboratory after a 2-week incubation period. However, young sexuales were found thriving on witch-hazel leaves in two enclosures (12 and 19 larvae, respectively) in the field.

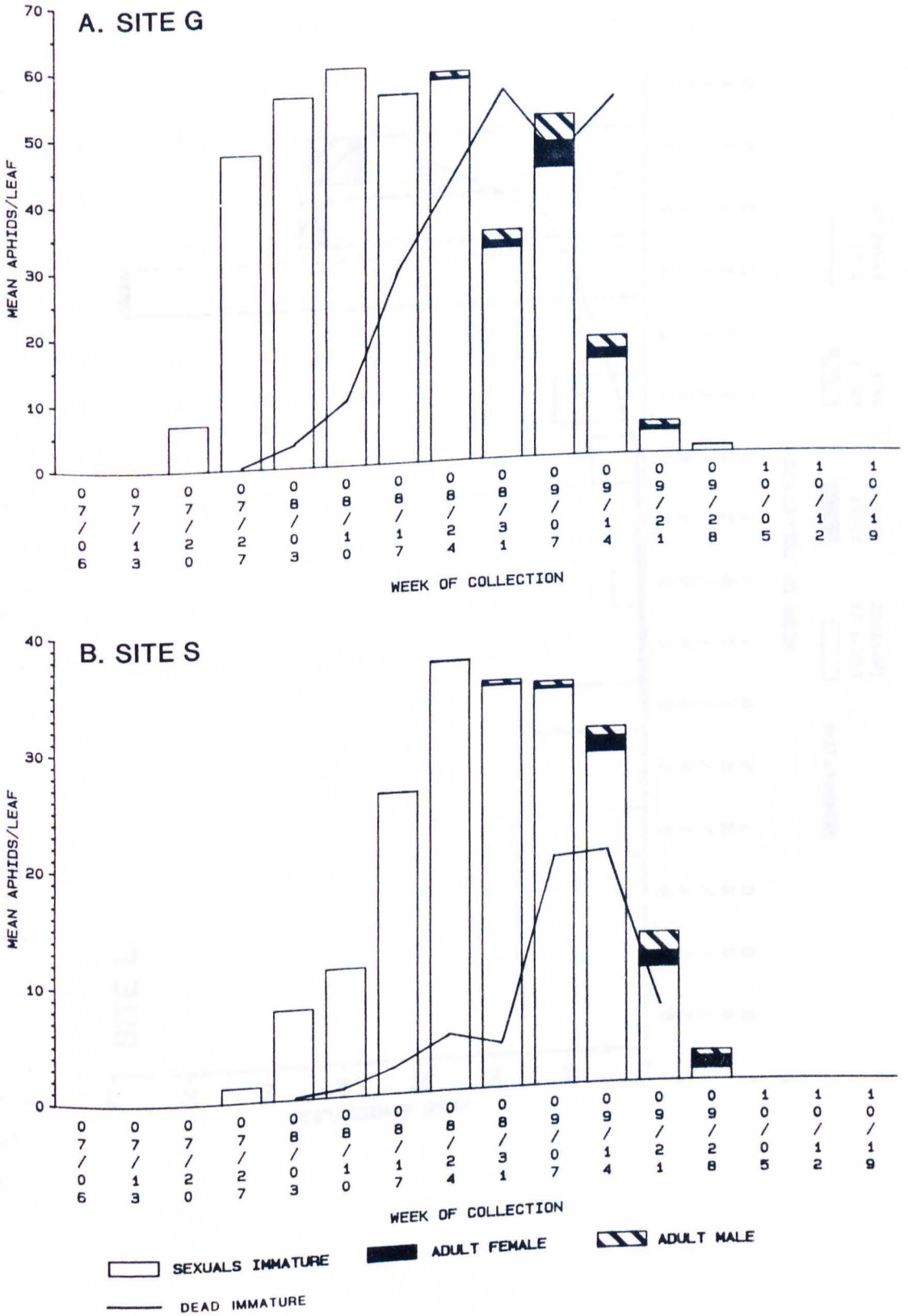
Lowland generation II alates given a choice of witch-hazel or river birch leaves selected river birch overwhelmingly if they chose to reproduce at all (Table 1). All offspring of lowland alates were aleurodiform larvae.

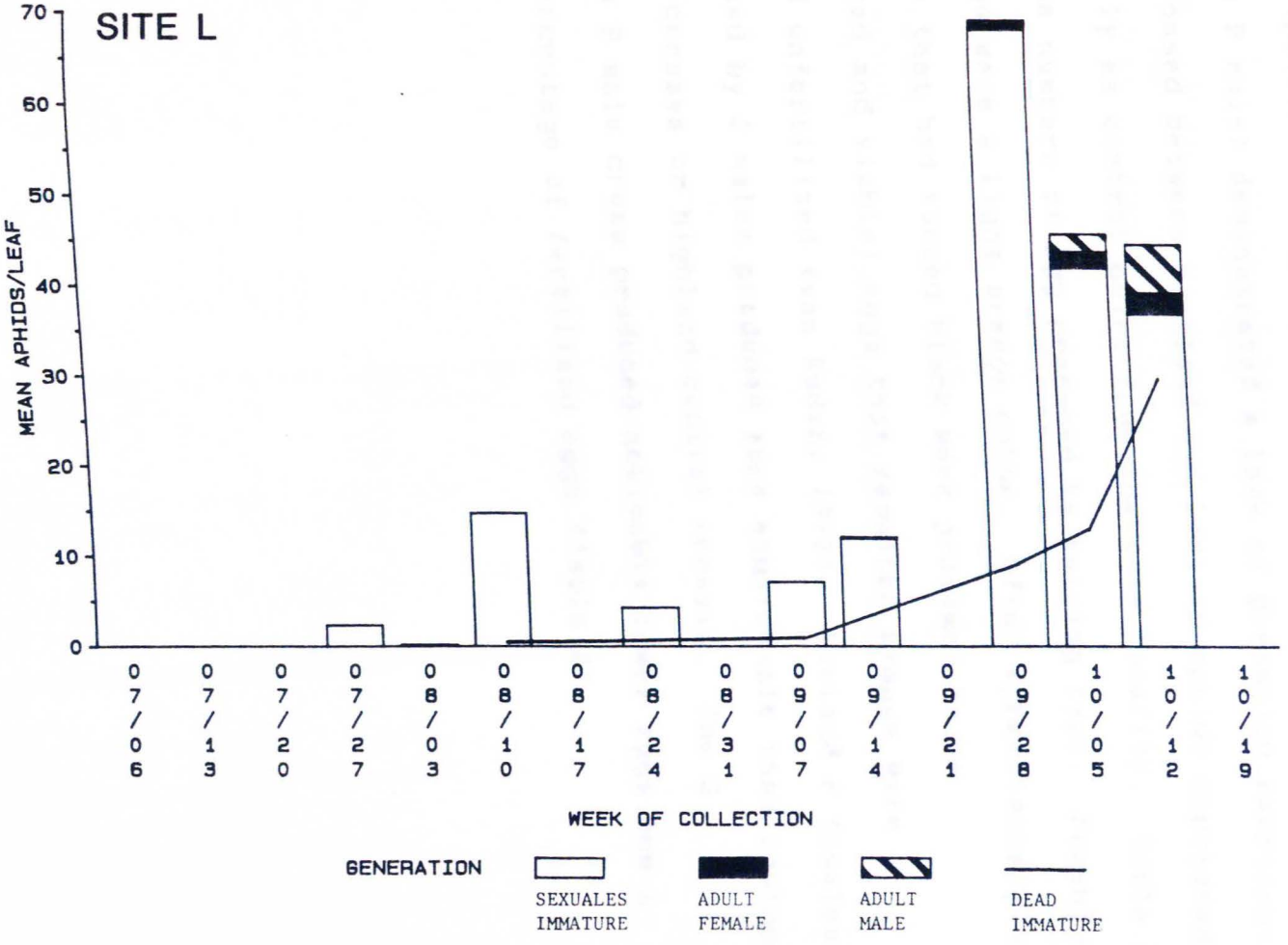
Figure 6. Weekly mean numbers per leaf of the lowland sexual generation (VII) aphids on witch-hazel at site P.

Figure 7. Weekly mean numbers per leaf of the highland sexual generation on witch-hazel. A. site G, B. site S.

Figure 8. Weekly mean numbers per leaf of the sexual generation on witch-hazel at intermediate elevation site L.


SITE P
MEAN APHIDS/LEAF
190
180
170
160
150
140
130
120
110
100
90
80
70
60
50
40
30
20
10
0
07/06
07/13
07/20
07/27
08/03
08/10
08/17
08/24
08/31
09/07
09/14
09/21
09/28
10/05
10/12
10/19
WEEK OF COLLECTION
GENERATION
SEXUALES IMMATURE
ADULT FEMALE
ADULT MALE
DEAD IMMATURE


A. SITE G
MEAN APHIDS/LEAF
0
10
20
30
40
50
60
70
07/06
07/13
07/20
07/27
08/03
08/10
08/17
08/24
08/31
09/07
09/14
09/21
09/28
10/05
10/12
10/19
WEEK OF COLLECTION
B. SITE S
MEAN APHIDS/LEAF
0
10
20
30
40
07/06
07/13
07/20
07/27
08/03
08/10
08/17
08/24
08/31
09/07
09/14
09/21
09/28
10/05
10/12
10/19
WEEK OF COLLECTION
SEXUALS IMMATURE
ADULT FEMALE
ADULT MALE
DEAD IMMATURE


SITE L
MEAN APHIDS/LEAF
70
60
50
40
30
20
10
0
07/06
07/13
07/20
07/27
08/03
08/10
08/17
08/24
08/31
09/07
09/14
09/21
09/28
10/05
10/12
10/19
WEEK OF COLLECTION
GENERATION
SEXUALES IMMATURE
ADULT FEMALE
ADULT MALE
DEAD IMMATURE

Experimental Cross-Mating of Lowland and Highland Sexuales

Reciprocal matings of both types (P female x G male, G female x P male) demonstrated a lack of premating barriers; pairs crossed between highland and lowland aphids copulated as readily as control pairs from the same locality. Table 2 shows the numbers of egg produced by pairing type. Freshly laid eggs were a light orange color. After approximately 48 hr, eggs that had turned black were presumed to be fertilized and viable; eggs that remained orange were presumed unfertilized (van Emden, 1972). Lowland P females fertilized by G males produced more eggs/female than lowland control crosses or highland control crosses. The G female x P male cross produced noticably fewer eggs and a lower percentage of fertilized eggs (Table 2).

Table 1. Lowland alate host-leaf choice in experimental chambers in the laboratory.

# Alates tested	# Alates bearing larvae	Larvae on RB[1] total	Larvae on RB[1] $\bar{X}$	Larvae on WH[2] total	Larvae on WH[2] $\bar{X}$
17	10	139	13.9	7	0.7

[1] WH = Witch-hazel
[2] RB = River birch
Note: All larvae on both WH and RB were virginoparous aleurodiform.

Table 2. Cross-mating of lowland and highland aphids on cut twigs in the laboratory.

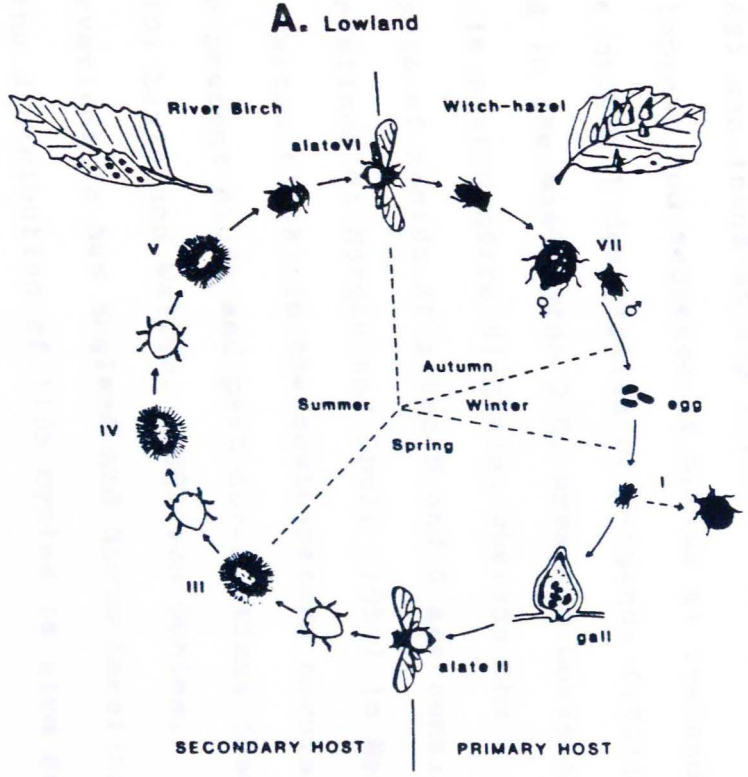
Pairing (F x M)	N (Female)	# Eggs Fertilized	# Eggs Unfertilized	Total Eggs/Female	% Eggs Fertilized
G x G (control)	17	70	0	4.11	100
P x P (control)	36	140	27	4.64	84
P x G (exper.)	45	182	48	5.11	79
G x P (exper.)	41	44	23	1.63	66

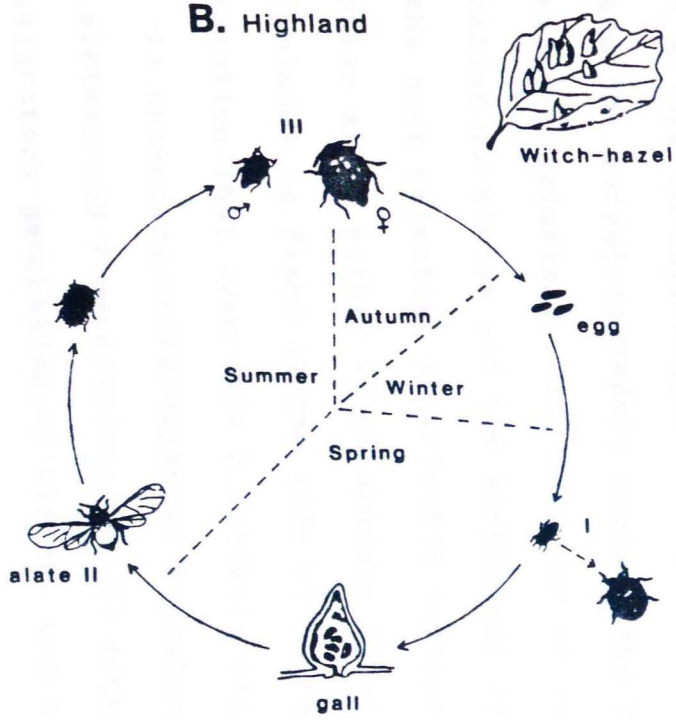
DISCUSSION

The quantitative, comparative study of Hormaphis hamamelidis in 4 locations provides unequivocal evidence for striking geographic variation in the life cycle of this aphid. The study at site P intentionally repeated Pergande's (1901) work at the original locality and in effect served as a control of the investigations at the other sites. That every detail of his report on the morphology and timing of the 7 developmental generations was confirmed by our field and laboratory methods permits us to interpret rigorously our observations at the other localities.

A composite picture of our interpretations of the 2 life cycle patterns is shown in Figure 9. Lowland (Figure 9a) fundatrices create large galls on witch-hazel in April and parthenogenetically produce virginoparous alates that emerge from galls in June and fly to the secondary host, river birch. These alates bear larvae of the first summer generation on birch; apterous, asexual, aleurodiform generations proliferate on birch throughout the summer, culminating in an alate, sexuparous generation that migrates back to witch-hazel in September. Sexual females and males are produced on witch-hazel and give rise to the overwintering eggs. In the highlands (Figure 9b), fundatrices and galls develop more slowly, parthenogenetic production of sexuparous generation II alates begins in June; the first alates emerge from galls in late July. The

Figure 9. The life cycle of Hormaphis hamamelidis. A. Lowland life cycle host-alternating between witch-hazel (primary host) and river birch (secondary host). B. Highland life cycle monoecious on witch-hazel only. [A, B, adapted from Pergande (1901), after Dixon (1985)].


A. Lowland
River Birch
Witch-hazel
alateVI
V
VII
♀
♂
Autumn
Summer
Winter
egg
Spring
IV
I
III
gall
alate II
SECONDARY HOST
PRIMARY HOST


B. Highland
Witch-hazel
III
♂
♀
Autumn
egg
Summer
Winter
Spring
I
alate II
gall

nonmigratory alates remain on witch-hazel to produce sexual offspring that mature in late August. Summer birch generations (and the normal secondary host, river birch) are absent in highland populations. The behavior of lowland and highland generation II alates and the morphology of their offspring in the host selection experiments indicates that their reproductive mode, either virginoparous (lowland), or sexuparous (highland) is fixed at the time of emergence from galls. The variation thus comprises 2 mutually exclusive alternatives: 1) heteroecy, virginoparous migratory generation II alates, and 7 generations, or 2) monoecy, sexuparous nonmigratory generation II alates, and 3 generations. No evidence of the 2-year life cycle proposed by Lampel (1968) was found at any site.

The development and sequence of aphids at lowland site P confirms the original description of Pergande (1901) for H. hamamelidis in the Washington D.C. area and Lewis and Walton (1958) in southeastern Virginia, whereas the abbreviated cycle of aphids at sites S and G are consistent with the observations of Morgan and Shull (1910) in New York and Lewis and Walton (1958) in the southwestern mountains of Virginia. The present study and past observations (Morgan and Shull, 1910; Lewis and Walton, 1958; von Dohlen, personal observations in New England and North Carolina), suggest that the distribution of life cycles is tied not only to altitude, but to latitude as well. The host-alternating, 7-generational form appears to be restricted to

low elevations and latitudes south of approximately 41oN; the monoecious, 3-generational form is restricted to higher altitudes and latitudes approximately 38oN or higher, except at high elevation where it extends further south. The distribution and abundance of lowland forms is undoubtedly dependent on the range of river birch, the secondary host, although alate aphids may disperse over surprisingly great distances (Taylor, Woiwod, and Taylor, 1979). Growing at low elevations only, river birch is reported to extend its range into southern New England (Brockman, 1979), although it was not found by Morgan and Shull (1910) in New York or by von Dohlen (personal observation) in Connecticut.

The fact that both lowland and highland forms of Hormaphis occur in sympatry at an intermediate elevation site (L) and retain their distinct life cycles strongly supports Borner's (1952) conclusion that the 2 forms are reproductively isolated species. Yet the 2 forms are fully compatible with respect to mating and oviposition in the laboratory and there is a brief opportunity (approximately 1 week at the end of September) when mature adult sexuales of both forms are synchronic and syntopic. However, because it is comparatively easy to interbreed aphid species and produce hybrids (Hille Ris Lambers, 1979) the outcome of the cross-mating experiments may have little to do with the taxonomic status of the 2 forms. It must also be noted that a few of the females collected for the experiment might not have been virgin; although most matings occurred on twigs,

sexual adults were on rare occasions observed to mate on the leaf surface. While our results indicate that there were no behavioral inhibitions to mating between highland and lowland aphids, the resulting egg numbers and percentages fertilized can be interpreted with less certainty. If the experimental females were indeed unmated before the experiment, the fact that most eggs from all crosses were black and apparently viable, limits still further the possible mechanisms of reproductive isolation, possibly through later zygote or larval inviability, or reduced fertility in F1 and F2 generations. Curiously, the dimorphic pattern in both gall and sexual generations at site L also matches Mordivilko's (1930a) speculation that within one species, early-opening galls produce virginoparae and late-opening galls produce sexuparae. We surmise the similarity is fortuitous.

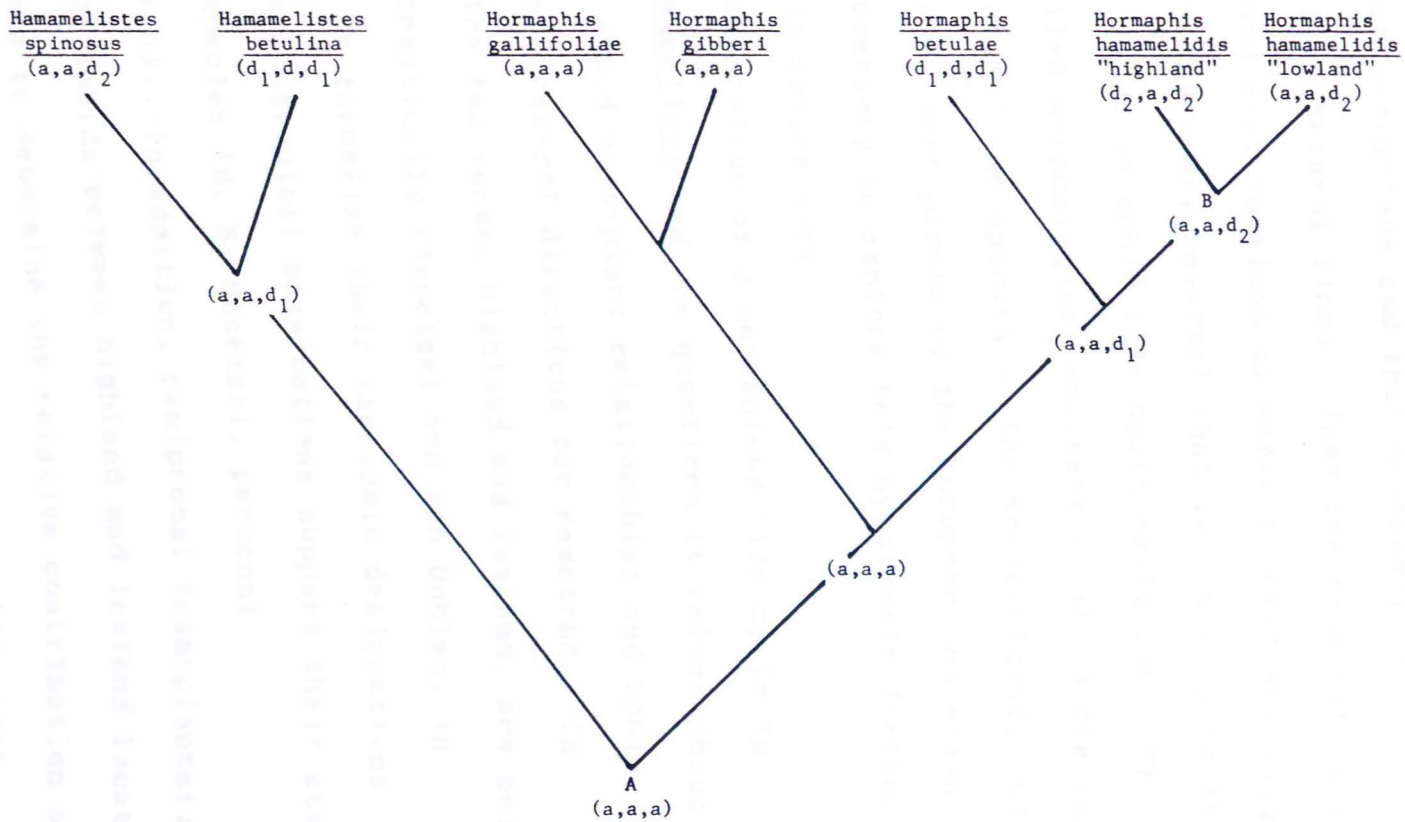
In H. hamamelidis, the presence of both host-alternating and monoecious life cycles on the same primary host raises the evolutionary question, which version is truly the ancestral state? The answer does not depend on whether highland and lowland forms are separate species or merely geographic races of one species; they clearly shared a common ancestor more recently than either did with any other species. Mordvilko (1928, 1930a,b, 1935a) has argued that the ancestral life cycle of H. hamamelidis must have been a monoecious one on Hamamelis that evolved in a subtropical climate where the host plant itself originated.

Betula, a temperate genus, gradually extended its distribution south as Hamamelis moved north. As the 2 host plants came into contact, migration to Betula by Hormaphis alates evolved first as a facultative, then obligatory transfer (Mordivilko, 1930a). Mordivilko (1930a,b) asserts that the first migrating forms must have been rare virginoparous alates that arose in galls among the normally sexuparous individuals; when migration to birch became possible, virginoparous forms gradually replaced the sexuparous gall alates and obligatory heteroecy was achieved. Monoecious forms of Hormaphis would have persisted on witch-hazel where suitable birch species were absent. Therefore, In Mordvilko's (1928, 1930a,b, 1935a) opinion and in the currently accepted view (Eastop, 1973a), aphids of the ancestral monoecious state inserted river birch as a secondary host and developed an obligate migration to it. In theory, a second possibility also exists: ancestral host-alternating forms, which themselves may have had monoecious ancestors, dropped the secondary host and all the generations became restricted to witch-hazel, thus creating a secondarily derived monoecious cycle. Such a secondary reversion to monoecy on the primary host is an evolutionary polarity undocumented in aphids.

It is useful to examine nearest relatives to gain insight into this question of evolution of Hormaphis life cycles. In North America, Hamamelistes spinosus is the next closest relative to H. hamamelidis, and is heteroecious

between witch-hazel and river birch (Pergande, 1901). Noted by Mordvilko (1930b, 1935b), two other Hormaphidine species in Europe and Asia, Hormaphis betulae and Hamamelistes betulina are anholocyclic on birch and closely resemble the apterous birch generations of Hormaphis hamamelidis and Hamamelistes spinosus, respectively. The only other recognized species in the Hormaphidini, Hormaphis gallifoliae and H. gibberi (Eastop and Hille Ris Lambers, 1976) are holocyclic and presumed to alternate between Hamamelis and Betula in Japan (Ghosh, 1985). Based on the available life cycle data and geographic distributions only, a preliminary sketch of the phylogenetic relationships between these aphids is drawn in Figure 10. The figure is not meant to represent a complete phylogenetic reconstruction of the tribe, but is intended as an hypothesis of the pattern of life cycle evolution in the Hormaphidini. The ancestral geographic location is assumed to be southeast Asia because it contains the majority of species of the subfamily Hormaphidinae (Mordvilko, 1924). The ancestral generation cycle is assumed to be holocyclic. Host-alternation between witch-hazel and birch is hypothesized to be the ancestral state of host use: it is more conservative (i.e. there are fewer character changes involved) to hypothesize that the common ancestor of Hormaphis and Hamamelistes (A) was host-alternating, the common ancestor

Figure 10. Preliminary phylogenetic reconstruction of the tribe Hormaphidini, based on available life cycle data and geographic distribution. (A,B,C) refers to the current states of the three characters in order (host, generation cycle, geographic location). The possible states are:
A (host): a, ancestral, host-alternation between witch-hazel and birch; d1, derived, on birch only; d2, derived, on witch-hazel only.
B (generation cycle): a, ancestral holocycle; d, derived anholocycle.
C (geographic location): a, ancestral, in Southeast Asia; d1, derived, in Europe and northern Asia; d2, derived, in North America.
(The states d1 and d2 may be derived independently from a).


Hamamelistes spinosus
(a,a,d_2)
Hamamelistes betulina
(d_1,d,d_1)
Hormaphis gallifoliae
(a,a,a)
Hormaphis gibberi
(a,a,a)
Hormaphis betulae
(d_1,d,d_1)
Hormaphis hamamelidis "highland"
(d_2,a,d_2)
Hormaphis hamamelidis "lowland"
(a,a,d_2)
B
(a,a,d_2)
(a,a,d_1)
(a,a,d_1)
(a,a,a)
A
(a,a,a)

of the lowland and highland forms of H. hamamelidis (B) was heteroecious and the monoecious highland form is derived, than to propose that the most recent ancestor of the two genera (A) was monoecious and that heteroecy arose independently in several lines. Thus the examination of the life cycles and distributions of nearest relatives suggests a possible evolutionary reversal that is contrary to the conventional views on aphid life cycle evolution. Of course, detailed morphological analyses of the different generations of all the species in the Hormaphidini, and confirmations of host plants of the European and Asian aphids are necessary to explore this hypothesis further, and are planned in future work.

The documentation of a monoecious life cycle in Hormaphis hamamelidis and the questions it raises about the evolution of aphid host-plant relationships and aphid life cycles suggests several directions for research. In particular, the two forms, highland and lowland, are being reviewed systematically (Stoetzel and von Dohlen, in preparation) to formalize their taxonomic designations. Preliminary morphological examinations support their status as separate species (M. B. Stoetzel, personal commununication). In addition, reciprocal transplantation experiments of aphids between highland and lowland locations are in progress to determine the relative contribution of genetic and environmental components to the life cycle variation. Regardless of the taxonomic designations of the

highland and lowland forms, the outcome of geographical transplantation experiments should provide valuable clues as to the nature of the anscestral form, if either of the two variants proves to be plastic in its life cycle. In an ecological perspective, future work will address reasons for the absence of the abbreviated life cycle in lowland habitats, for which no satisfactory explanation so far exists.

REFERENCES

Aoki, S. 1977. Colophina clamatis (Homoptera, Pemphigidae), an aphid species with 'soldiers'. Kontyu 45:276-282.

Blackman, R.L. 1972. The inheritance of life-cycle differences in Myzus persicae (Sulz.) (Hem., Aphididae). Bulletin Entomological Research 62:281-294.

Blackman, R.L. 1974. Life-cycle variation of Myzus persicae (Sulz.) (Hom. Aphididae) in different parts of the world, in relation to genotype and environment. Bulletin Entomological Research 63:595-607.

Blackman, R.L. 1975. Photoperiodic determination of the male and female sexual morphs of Myzus persicae. Journal Insect Physiology 21:435-453.

Blackman, R.L., and V.F. Eastop. 1984. Aphids on the World's Crops: An Identification and Information Guide. John Wiley and Sons, New York. 413 pp.

Blackman, R.L. and A.J.C. Paterson. 1986. Separation of Myzus (Nectarosiphon) antirrhinii (Macchiati) from Myzus (N.) persicae (Sulzer) and related species in Europe (Homoptera: Aphididae). Systematic Entomology 11:267-276.

Börner, C. 1952. Europae centralis Aphides. Mitteilungen der Thuringeschen Botanischen Gesellschaft 4(3):1-488.

Brockman, C.F. 1979. Trees of North America, A guide to Field Identification. Golden Press, New York.

Davidson, J. 1927a. On the biological and ecological aspects of migration in Aphides. I. Science Progress in the Twentieth Century 21:641-658.

Davidson, J. 1927b. On the biological and ecological aspects of migration in Aphides. II. Science Progress in the Twentieth Century 22:57-69.

Dixon, A.F.G. 1971. The "interval timer" and photoperiod in the determination of parthenogenetic and sexual morphs in the aphid Drepanosiphum platanoides. Journal Insect Physiology 17:251-260.

Dixon, A.F.G. 1985a. Aphid Ecology. Blackie, Glasgow.

Dixon, A.F.G. 1985b. Structure of aphid populations. Annual Review Entomology 30:155-174.

Dixon, A.F.G. and D.N. Glen. 1971. Morph determination in the bird cherry-oat aphid. Annals Applied Biology 68:11-21.

Eastop, V.F. 1973a. Deductions from the present day host plants of aphids and related insects. In H.F. van Emden, ed., Insect/Plant Relationships. Symposium Royal Entomological Society of London 6:157-178 .

Eastop, V.F. 1973b. Biotypes of aphids. pp. 40-51 in A.D. Lowe, ed., Perspectives in Aphid Biology. Bulletin 2. The Entomological Society of New Zealand (Inc.).

Eastop, V.F. and D. Hille Ris Lambers. 1976. Survey of the World's Aphids. W. Junk, The Hague. 573 pp.

Fitch, A. 1851. Catalogue of the Homopterous Insects of New York.

Ghosh, A.K. 1985. Hormaphidinae: distribution, phylogeny and systematics. Proceedings International Aphidological Symposium, Jablonna, 1981. Zaklad Narodowy im. Ossolinskich Wydawnietwo, Wroclaw.

Guldemond, J.A. (in press). Biosystematics of the Cryptomyzus Oestland complex: Some preliminary results on host plant acceptance, electrophoretic variation and reproductive isolation. International Symposium on Population Structure, Genetics and Taxonomy of Aphids. Smoloenice, 1985.

Hille Ris Lambers, D. 1950. Hostplants and aphid classification. Proceedings 8th International Congress Entomology, Stockholm. pp. 141-144.

Hille Ris Lambers, D. 1966. Polymorphism in Aphididae. Annual Review Entomology 11:47-78.

Hille Ris Lambers, D. 1979. Aphids as botanists? Symposium Bot. Upsal. 22(4):114-119.

Johnson, B. 1965. Wing polymorphism in aphids. II. Interaction between aphids. Entomologia Experimentale et Applica. 8:49-64.

Kennedy, J.S. and H.L.G. Stroyan. 1959. Biology of aphids. Annual Review Entomology 4:139-160.

Kenten, J. 1955. The effect of photoperiod and temperature on reproduction in Acyrthosiphon pisum (Harris) and on the forms produced. Bulletin Entomological Research 46:599-624.

Lampel, G. 1968. Die Biologie des Blattlaus Generationwechsels. Gustav Fischer Verlag.

Lees, A.D. 1959. The role of photoperiod and temperature in the determination of parthenogenetic and sexual forms in the aphid Megoura viciae Buckton. I. The influence of these factors on apterous virginoparae and their progeny. Journal Insect Physiology 3:92-117.

Lees, A.D. 1966. The control of polymorphism in aphids. Advances in Insect Physiology 3:207-277.

Lewis, I.F. and L. Walton. 1958. Gall formation on Hamamelis virginiana resulting from material injected by the aphis, Hormaphis hamamelidis (Fitch). Transactions American Microscopy Society 77-146-200.

MacGillivray, M.E. 1972. The sexuality of Myzus persicae (Sulzer), the green peach aphid, in New Brunswick (Homoptera: Aphididae). Canadian Journal Zoology 50:469-471.

MacGillivray, M.E. and G.B. Anderson. 1964. The effect of photoperiod and temperature on the production of gamic and agamic forms in Macrosiphum euphorbiae (Thomas). Canadian Journal Zoology 42:491-510.

Markkula, M. 1963. Studies on the pea aphid, Acyrthosiphon pisum Harris (Hom., Aphididae) with special reference to the difference in the biology of the green and red forms. Ann. Agric. Fenn. 2:1-29.

Mordvilko, A.K. 1924. On the history of some groups of aphids. Transactions 4th All Russian Entomological and Phytopathological Conference, 1924. pp. 180-186.

Mordvilko, A.K. 1928. The evolution of cycles and the origin of heteroecy (migrations) in plant-lice. Annals and Magazine of Natural History (series 10) 12:570-582.

Mordvilko, A.K. 1930a. About the origin of heteroecy in plant-lice. Comptes Rendus de l'Academie des Sciences de l'URSS 1930: 256-262.

Mordvilko, A.K. 1930b. Aphids of the subtribe Hormaphidina. Comptes Rendus de l'Academie des Sciences de l'URSS. 1930(A):168-172.

Mordvilko, A.K. 1935a. Aphids: their generation cycles and evolution. Priroda 11:35-44.

Mordvilko, A.K. 1935b. Aphids with an incomplete cycle of generations and their evolution. Entstehung. Ergebn. Fortschr. Zool. 8:36-328.

Morgan, T.H. and A.F. Shull. 1910. The life cycle of Hormaphis hamamelidis. Annals Entomological Society of America 3:144-146.

Müller, F.P. 1985. Biotype formation and sympatric speciation in aphids (Homoptera: Aphididae). Entomologia Generalis 10:161-181.

Pergande, T. 1901. The life history of two species of plant-lice inhabiting both the witch-hazel and birch. U.S. Department of Agriculture Technical Series 9:7-44. Government Printing Office, Washington, D.C.

Taylor, L.R., I.P. Woiwod, and R.A.J. Taylor. 1979. The migratory ambit of the hop aphid and its significance in aphid population dynamics. Journal of Animal Ecology 48:955-972.

Shaposhnikov, G.Ch. 1959. Initiation and evolution of the change of hosts and diapause in plant lice (Aphididae) in the course of the adaptation to the annual cycles of their host plants. Ent. Obozr. 38(3):435-452.

Shaposhnikov, G.Ch. 1981. Populations and species in aphids and the need for a universal species concept. Special Publication Research Branch Agriculture Canada. 61 pp.

Shaposhnikov, G.Ch. 1984. Aphids and a step toward the universal species concept. Evolutionary Theory 7:1-39.

van Emden, H.F. Aphid Technology, with special reference to the study of aphids in the field. Academic Press, London. 344 pp.

Chapter 2

Intraspecific interactions and host-plant relations of the witch-hazel leaf gall aphid, *Hormaphis hamamelidis*, on witch-hazel, *Hamamelis virginiana*

List of Tables

List of Figures

INTRODUCTION

The comprehensive program of research on the interaction between the gall-making aphid Pemphigus betae Doane (Pemphiginae) on the narrowleaf cottonwood Populus angustifolia (Whitham, 1978, 1979, 1980, 1986) has produced a compelling case of a complex insect-host plant interaction. First-instar fundatrices (founders of a parthenogenetic clone) form galls on leaves of the cottonwoods and display specific aggressive and discriminatory behaviors that enable them to find and colonize microhabitats within individual trees with the potential for the greatest reproduction (Whitham, 1978, 1980, 1986). Microhabitat selection appears to be influenced ultimately by leaf size, by physical contests between competing fundatrices, and more proximately by sensory assessment of suitable sites (Whitham, 1986). Aphids in larger galls enjoy enhanced fecundity and produce larger and faster-developing offspring that are more fecund at maturity (Whitham 1978, 1980). On multiple-galled leaves, fundatrices in those galls most proximal to the petiole are markedly more successful by several measures of relative fitness than are aphids in more distally positioned galls (Whitham, 1978, 1980). Whitham (1979, 1986) argues convincingly that it is this density-dependent, gall position-dependent variance in net reproductive success among fundatrices that has driven the evolution of territorial behavior in P. betae, whereby the most favorable

settling sites are defended against competing individuals. Thus, direct behavioral and competitive interactions generated by heterogeneity among and within leaves result in significant differentials in aphid reproductive performance.

The purpose of this study was to evaluate the importance of density- and position-dependent factors on the population ecology of another gall-inducing aphid. Only distantly related to P. betae, aphids of the tribe Hormphidini in the subfamily Hormaphidinae, a sister group to the Pemphiginae, form characteristic galls on species in the Hamamelidaceae. The specific system of Hormaphis hamamelidis (Fitch) on witch-hazel, Hamamelis virginiana, was studied to assess the importance of gall position, gall density, leaf size, and gall size on aphid reproductive success, and the ways in which these factors might interact. This report is part of a larger investigation of the factors responsible for the evolution of diverse life histories in the Hormaphidine aphids (von Dohlen and Gill, MS).

Biology of Hormaphis hamamelidis

The life cycle of Hormaphis hamamelidis (Fitch) was originally described (Pergande 1901) as a complex cycle that included seven generations and a host-alternation between witch-hazel and river birch, Betula nigra. von Dohlen and Gill (MS) have confirmed this description at the original locality along the Potomac River 10 miles north of Washington, D.C. but have also discovered an alternative

cycle (3 generations, not host-alternating) at higher elevation sites in western Virginia (ibid.). This abbreviated life cycle matches descriptions of short life cycles by Morgan and Shull (1910) in New York, Lewis and Walton (1958) in southwestern Virginia, and may extend into New England (von Dohlen, personal observation). The two forms are currently under systematic review (Stoetzel and von Dohlen, in preparation). For this paper the two life cycles will be referred to as "highland" (single host) and "lowland" (host-alternating) forms.

Hormaphis hamamelidis overwinters as eggs laid in bark crevices of host witch-hazel bushes and hatch in early spring, approximately 2 weeks before leaf bud break. Newly hatched fundatrices crawl to closed leaf buds and may wait for days or weeks for the leaves to unfold. As the buds burst and leaves expand, the fundatrices probe the leaf undersurfaces. The stimulus of a fundatrix eventually promotes a protruding, cone-shaped pouch gall to develop on the dorsal side of the leaf (Pergande, 1901; Lewis and Walton 1958). Fundatrices have not yet been observed to migrate among buds after the leaves have begun to expand, implying that aphids have made their settling decision by the time of bud break. Fundatrices mature inside the gall and produce the second generation by parthenogenetic reproduction (Pergande, 1901). Mature alates of the second generation depart from galls and migrate to river birch (lowland) (Pergande, 1901; von Dohlen and Gill, MS) or

remain on witch-hazel (highland) (Lewis and Walton, 1958; von Dohlen and Gill, MS). During this study gall densities were low, galls were commonly found singly on leaves, and heavily infested bushes were rare.

METHODS

Samples were collected at 3 locations in Virginia. Two study sites were at high elevation: site G, 1000 m in the Shenandoah Mountains (George Washington National Forest), northwestern Virginia, and site S at 1000 m in the Blue Ridge Mountains (Shenandoah National Park, Central Section) in north- central Virginia. The third site was essentially at sea level along the Potomac River in the Dranesville District Park, Dranesville, Virginia. Witch-hazel was a dominant understory shrub or small tree at all sites (see von Dohlen and Gill, MS, for further details of the study sites).

In April 1986 at sites G and S, and March 1986 at site P, witch-hazel bushes were monitored during the aphid hatching period. The behavior of first-instar fundatrices was closely observed on the unopened leaf buds and later on the developing leaves as aphids began to form their galls.

Only the first 2 gall generations on witch-hazel were considered for this study because these generations are entirely comparable between the 2 forms. For the analyses of the relationships between gall position, gall size, leaf size, and fundatrix fecundity, witch-hazel leaves with Hormaphis galls were collected on July 11, 17, 25, and August 2, 1986 at site G, on July 25, 1986 at site S, and on May 16, 22, and 28, 1986 at site P. At site G, these sample dates represented the weeks asymptotic to peak reproduction and included 2 dates when the first few mature alates were

found in galls (von Dohlen and Gill, MS). The sample at site S was collected at the first observation of mature alates in galls. Samples at sites G and S consisted of 5 leaves with single galls from each of 6 tagged witch-hazel shrubs (30 total per site per sample date). At site P the sample dates were also asymptotic to peak reproduction, and just before the galls suffered substantial predation (von Dohlen and Gill, MS); the last sample date included galls containing the first few mature alates. Each sample at site P consisted of 5 leaves from each of 5 tagged bushes (25 total per sample).

From one heavily galled tree at site S, samples of witch-hazel leaves with varying densities of Hormaphis galls were collected on July 11, 17, 25, and August 2, 1985 as follows: 8 leaves with single galls, 4 leaves with two galls, 2 leaves with 4 galls, 1 leaf with 8 galls and 1 leaf with 16 galls. These collection dates were also during the period asymptotic to peak reproduction at that site.

Galled leaves were picked from all parts of the shrubs in order to include all possible within-bush microclimates. Samples were transported to the laboratory in coolers with ice and stored in the refrigerator at 5oC. Analysis of samples was completed within 24-48 hr of collection.

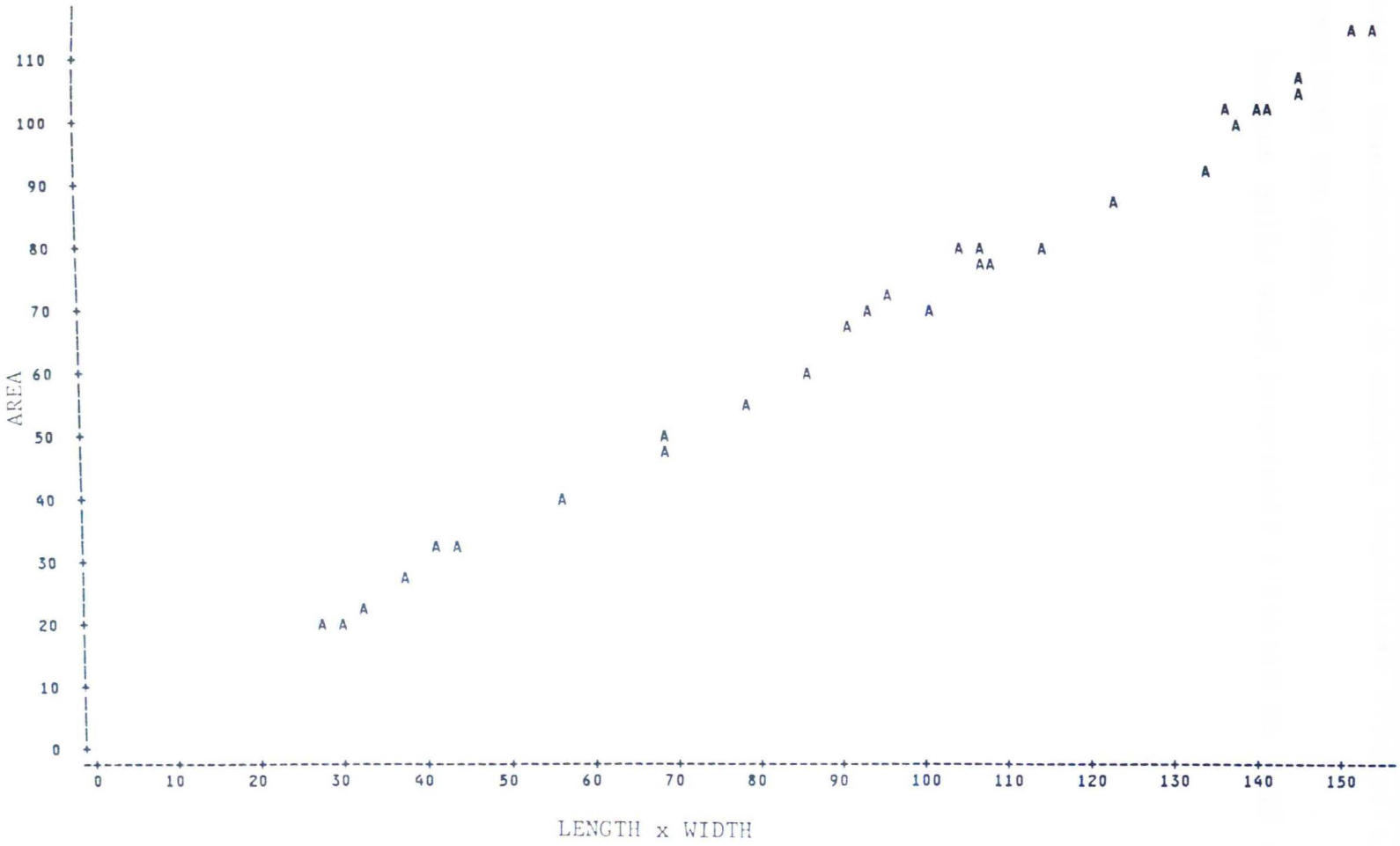
Leaf size was determined by measuring leaf length from tip to petiole insertion, and greatest leaf width. Leaf measurements were converted to area by the linear equation area=-0.38+0.73*(length*width). To obtain this equation, 30

mature leaves were first measured for length and width, then passed through a leaf area meter (Lambda Instruments Co., model LI3000) for actual area. Correlation analysis was performed on length*width with actual area and was highly significant ($r=.997$, $p<.0001$; Figure 1). The significant regression of length*width on area ($r2=.994$, $p<.0001$) provided the linear equation to calculate leaf area.

The gall dimensions were measured with calipers: a) height from gall tip (above upper leaf surface) to base (lowest point below leaf undersurface), and b) width at widest girth above upper leaf surface. Heights and widths were then translated to an index of gall size by the equation $pi*r(r2+h2)1/2$, the lateral surface area of a cone. This index was biologically meaningful for Hormaphis aphids because galls were cone-shaped, and aphids fed on the inside surface area of the gall "walls," but not on the "floor" of the gall. Both leaf and gall area were transformed to square-roots before analysis to conform to a linear scale and to normalize the data.

Each gall was opened lengthwise and the residents (generation I fundatrix and her parthenogenetic generation II progeny) were gently transferred with a paintbrush to filter paper and counted under 80x with a Wild dissecting microscope. Generation II progeny were recorded as either immature nymphs or as winged adults. Fecundity was

Figure 1. The correlation of length x width to actual area (measured with a leaf area meter) of a sample of 30 witch-hazel leaves; $r=.997$, $p<.0001$.


AREA
LENGTH x WIDTH
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150

calculated as [generation II immature + generation II adult]; transforming to natural logarithms (fecundity + 1) normalized the data.

Because galls were invariably situated on leaf veins, gall position on the leaf was recorded by 1) vein number (counting alternate veins distally from the petiole insertion) and 2) position on the central vein or distance from it by quartiles (0=exactly on central vein, 1=quartile nearest central vein, ..., 4=quartile at leaf edge). For statistical analysis a single index of gall position was derived by adding vein number and quartile together.

Statistical Analysis

Consideration of probable cause-and-effect relationships among the features analyzed in this study (gall position, gall density, gall size, final leaf area, and maximum aphid reproduction) dictated the choice of statistical analyses, whether regression, correlation, or analysis of variance procedures were used. Because fundatrices were not observed to shift position on the expanding leaves as they initiated their galls at bud break, gall position seemed to be fixed before final leaf area or gall size were determined. Therefore, neither leaf area, gall size, nor aphid fecundity could have been causal agents of gall position, but the position of galls could have affected the processes of leaf expansion and gall development and the rates of reproduction of aphids, hence

regression was employed. Fundatrix densities on the leaf buds could have affected the selection of gall sites, but the positions of aphids already occupying a bud also could have influenced the numbers of newly arriving aphids during the hatching period. Thus, density and gall position could have been reciprocally interactive, and were therefore analyzed by correlation. After aphids had settled and begun their galls, final leaf area, gall area, and aphid reproduction could have been influenced by gall density; the effect of density on these variables was assessed by analysis of variance. Because galls grew and leaves expanded at the same time they were expected to have mutual correlated effects upon one another. In addition, because leaf expansion was completed long before significant (any in highland populations) aphid reproduction occurred, aphid reproduction itself was not expected to affect leaf area, but variation in leaf area could have been a determining factor of the variation in aphid fecundity; thus regression analysis was used. Gall growth and aphid reproduction proceded simultaneously and therefore could have been mutually interactive and correlated. The variation among study sites of gall position, gall size, leaf area, and gall area was appropriately analyzed by analysis of variance, as was the among-bush (within-site) variation in gall position.

Only healthy galls without predators were included in the statisical analyses. All data analyses were performed on the University of Maryland's IBM computer with the SASR

Version 5 (1985) edition statistical program. The variation among study sites in gall position, gall area, leaf area, and fecundity were analyzed separately with analysis of variance (ANOVA) and Student-Newman-Keuls (SNK) multiple comparisons test with the SAS General Linear Models (GLM) procedure. Among-bush variation in gall position within sites was analyzed with ANOVA and Student-Newman-Keuls. Analyses of covariance (ANCOVAs) on leaf area and gall position, gall area and gall position, fecundity and gall position, and fecundity and leaf area were performed with the SAS GLM. The assumption of homogeneity of slopes was tested (and satisfied) prior to all ANCOVA procedures. Multiple comparisons of mean leaf area, gall area, and fecundity among bushes (pooled over sample dates) were performed post-ANCOVA with the SNK procedure. Correlation analyses of leaf area with gall area, fecundity with gall area, and gall position with density were analyzed separately for each collection date. The relationships of gall area, leaf area, and fundatrix fecundity to gall density were analyzed separately by nested ANOVA (GLM for nested design and unequal sample sizes). The GT2-method for multiple comparisons of means with unequal sample sizes (Sokal and Rohlf, 1981) was carried out post-ANOVA on density means for leaf area, gall area, and fecundity.

RESULTS

The behavior of fundatrices in early spring, 1986 (late March at site P, mid-April at sites G and S) after hatching and during colonization of unopened leaf buds was consistent at the three locations. Upon hatching, aphids crawled out to the leaf buds and waited for them to expand. The young fundatrices were not observed to engage in physical contests or exhibit other territorial behaviors on the buds or leaves. Even on those rare bushes where aphids reached high densities (some buds supporting >20 aphids) fundatrices did not appear to interact. At both high and low densities, mature galls were found abutting one another and occasionally were partially grown together.

Galls at lowland site P were positioned significantly closer to the petiole than were galls at either highland site G or S (Table 1). As expected, gall position was not significantly variable among sample dates at sites G and P (ANOVA, site G: error df=119, F=.18, p=.91; site P: error df=49, F=.08, p=.92); gall position did not vary significantly among bushes within sites (Table 1).

On multiple-galled leaves (analysis possible at site S only) the density of fundatrices (=galls) per leaf and the positions they chose did not measurably influence one another (Table 2a). Correlation analysis confirmed that gall position was not significantly correlated with gall density (r=.085, p=.288, N=158).

Table 1. A. Gall position: mean, one standard error, and sample size for replicate bushes during the period of asymptotic peak reproduction at sites G, S, and P. Data are pooled across sample dates.
B. ANOVA of gall position among sites. Data were from the sample date at each site when mature alates were first observed in galls. Site G and S, date = 25 July, 1986; site P, date = 28 May, 1986.

A.

Site G				Site S				Site P			
Bush	$\bar{X}$	SE	N	Bush	$\bar{X}$	SE	N	Bush	$\bar{X}$	SE	N
G1	8.65	.71	20	S1	8.00	1.38	5	P1	6.91	.68	11
G2	8.08	.35	20	S2	5.00	.84	5	P2	5.38	.55	13
G3	8.33	.44	20	S3	8.60	2.06	5	P3	4.87	.39	15
G4	7.65	.60	20	S4	8.10	.56	5	P4	5.83	.52	12
G5	7.00	.44	20	S5	9.25	1.43	4	P5	6.92	.56	13
G6	7.95	.55	20	S6	8.00	1.41	5				
Total	7.44	.57			7.83	1.47			5.98	.92	

B.

Source of Variation	df	MS	F.	p
Site	2	25.47	3.95	.025*
Bush(Site)	14	6.82	1.06	.41 (NS)
Error	59	6.45		
Total	75			

SNK[1]

Site	$\bar{X}$	Grouping	N
G	7.88	A	30
S	7.78	A	29
P	5.76	B	17

[1]Student-Newman-Keuls test groupings of means post-ANCOVA; means with the same letter are not significantly different; A>B>C.

Table 2. Impact of gall density per leaf on gall position, leaf area, gall area, and fundatrix fecundity: mean, one standard error, sample size, and GT2 groupings during four weeks of asymptotic peak reproduction from one bush at site S, July-August 1985.

Date:	11 VII			20 VII			27 VII			2 VIII			
	$\bar{X}$	SE	N	$\bar{X}$	SE	N	$\bar{X}$	SE	N	$\bar{X}$	SE	N	GT2[1]
A. Gall Position:													
Density													
1	7.43	1.36	7	7.13	1.09	8	6.63	1.05	8	7.28	0.97	7	-
2	9.29	0.68	7	7.29	1.27	7	8.88	0.90	8	6.83	1.08	6	-
4	6.75	1.03	4	8.67	0.99	6	5.00	0.64	7	5.63	1.07	8	-
8	7.29	0.75	7	7.29	1.21	7	6.00	1.38	5	9.50	1.57	6	-
16	7.40	0.60	15	6.10	0.95	10	9.64	0.82	11	8.21	0.41	14	-
B. Leaf Area (cm^2):													
Density													
1	68.81	9.14	7	52.33	4.30	8	53.47	3.08	8	69.38	10.39	7	A
2	81.17	10.45	4	55.54	2.51	4	53.56	8.11	4	54.32	5.00	4	A
4	57.47	8.58	2	40.81	1.22	2	37.34	14.18	2	64.52	14.41	2	A
8	25.42	0	1	41.60	0	1	52.68	0	1	52.90	0	1	A
16	36.41	0	1	46.22	0	1	39.83	0	1	26.67	0	1	A
C. Gall Area (mm^2):													
Density													
1	56.23	4.54	7	59.38	4.54	8	64.89	6.64	8	72.65	7.41	7	A
2	54.01	6.99	7	54.23	6.73	7	51.71	3.12	8	64.27	6.14	6	AB
4	47.44	7.47	4	55.47	9.24	6	51.70	6.69	7	64.24	4.73	8	AB
8	50.06	4.95	7	57.44	4.01	7	57.04	9.48	5	63.06	5.28	6	AB
16	61.62	3.68	15	38.90	3.50	10	43.59	3.50	11	46.66	2.26	14	B
D. Fecundity:													
Density													
1	26.57	3.93	7	38.63	3.93	8	41.13	6.13	8	33.86	6.15	7	A
2	23.71	2.59	7	28.43	4.61	7	37.13	3.57	8	33.33	5.77	6	AB
4	13.25	3.35	4	33.00	8.92	6	32.14	2.50	7	38.00	4.19	8	AB
8	22.71	4.40	7	34.29	3.12	7	34.00	4.83	5	44.50	4.90	6	AB
16	22.67	2.55	15	21.70	2.94	10	23.00	3.13	11	22.07	2.53	14	B

[1]GT2 test groupings post-ANOVA of density means pooled over sample dates, using the leaf(date dens) variance as an error term; densities with the same letter are not significantly different; A>B.

Final leaf area was variable among sites (Table 3); leaves at site S were significantly larger than at G or P (Table 3b). Sample date did not contribute significantly to the variance in leaf area at sites G and P (Table 4). Final leaf area of galled leaves varied among bushes at sites G and P, but not at site S (Table 4). At sites G and P, final leaf area was significantly affected by gall position (Figures 2a and 2c, Table 4): leaves with galls closer to the petiole were smaller. The relationship of leaf area and gall position at site S (Figure 2b) was also negative, but just missed statistical significance (Table 4). Because the total number of veins on a leaf and leaf area were not significantly correlated ($r=.074$, $p=.70$, $N=30$), gall position was not simply an artifact of the number of veins available for colonization on large versus small leaves. Gall density per leaf significantly depressed leaf growth overall (Table 2b, 5), but the conservative GT2 procedure was unable to discriminate among the means of leaf sizes at the 5 densities (Table 2b). Final leaf area and gall area were not significantly correlated at any site (Table 6a, Figure 3).

Galls grew to significantly larger sizes at site P than at G or S (Table 7), even though gall area varied significantly among bushes at all sites (Tables 7b, 8). Gall size increased significantly over sample dates at site P only, although the significant date*bush interaction indicates that the galls on individual bushes were growing

Table 3. A. Leaf area (cm^2): mean, one standard error, sample size and SNK groupings for replicate bushes during the period of asymptotic peak reproduction at sites 6 and S in July-August, 1986, and site P in May, 1986.
B. ANOVA among sites of leaf area (cm; square-root transformed). Data were from the sample date at each site when mature alates were first observed in galls. Site 6 and S, date = 25 July, 1986; site P, date = 28 May, 1986.

A.

		Site 6					Site S			Site P				
		Date:					Date:			Date:				
Bush		11 VII	17 VII	25 VII	2 VIII	SNK[1]	Bush	25 VII	SNK[1]	Bush	16 V	22 V	28 V	SNK[1]
61	$\bar{X}$:	40.28	40.73	43.84	32.35	BC	S1	74.37	A	P1	34.49	49.46	51.59	A
	SE:	3.82	4.09	17.86	.72			9.13			11.59	11.09	12.75	
	N:	5	5	5	5			5			3	5	3	
62	$\bar{X}$:	52.57	52.82	60.03	53.18	A	S2	66.34	A	P2	47.79	34.39	30.91	AB
	SE	9.59	9.04	6.56	10.90			20.11			7.16	8.69	11.56	
	N:	5	5	5	5			5			5	5	3	
63	$\bar{X}$:	35.51	44.58	36.93	48.94	B	S3	56.61	A	P3	45.70	20.24	22.55	B
	SE:	2.42	9.55	5.60	7.25			10.91			8.48	4.50	5.22	
	N:	5	5	5	5			5			5	5	5	
64	$\bar{X}$:	38.52	38.21	39.10	38.70	BC	S4	72.01	A	P4	57.23	50.62	56.07	A
	SE:	5.60	5.64	3.07	5.80			14.59			9.94	10.74	11.64	
	N:	5	5	5	5			5			4	5	3	
65	$\bar{X}$:	34.65	29.36	29.22	29.93	C	S5	88.49	A	P5	61.82	38.29	68.21	A
	SE:	6.18	5.95	5.37	4.46			13.06			12.04	10.17	15.71	
	N:	5	5	5	5			4			5	5	3	
66	$\bar{X}$:	57.04	45.87	50.56	63.03	A	S6	79.76	A					
	SE:	6.52	8.51	3.96	4.71			15.16						
	N:	5	5	5	5			5						
Total	$\bar{X}$:	43.10	40.93	43.28	44.36			72.93			49.39	38.60	45.87	
	SE:	9.40	9.95	10.86	12.90			10.97			10.69	12.42	18.73	

B.

Source of Variation	df	MS	F_m	p
Site	2	31.54	10.48	.0001***
Bush(Site)	14	4.57	1.52	.13 (NS)
Error	59	3.01		
Total	75			

SNK[1]

Site	$\bar{X}$	Grouping	N
6	6.40	B	30
S	8.29	A	29
P	6.26	B	17

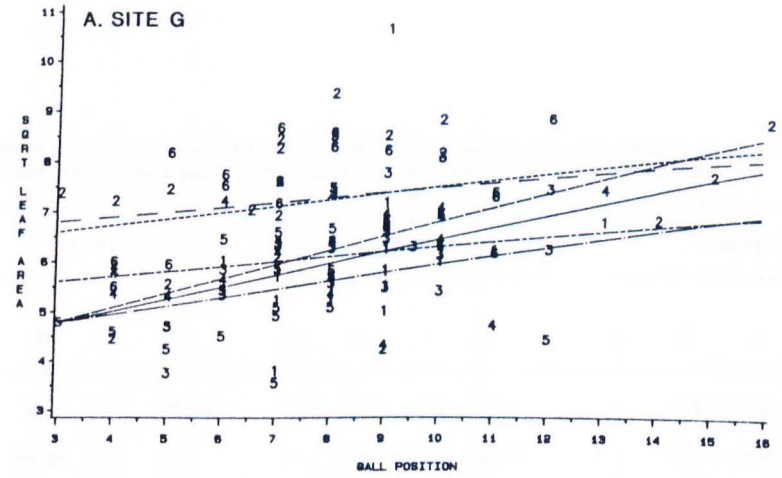
[1]Student-Newman-Keuls test groupings of means post-ANCOVA; means with the same letter are not significantly different; A>B>C.

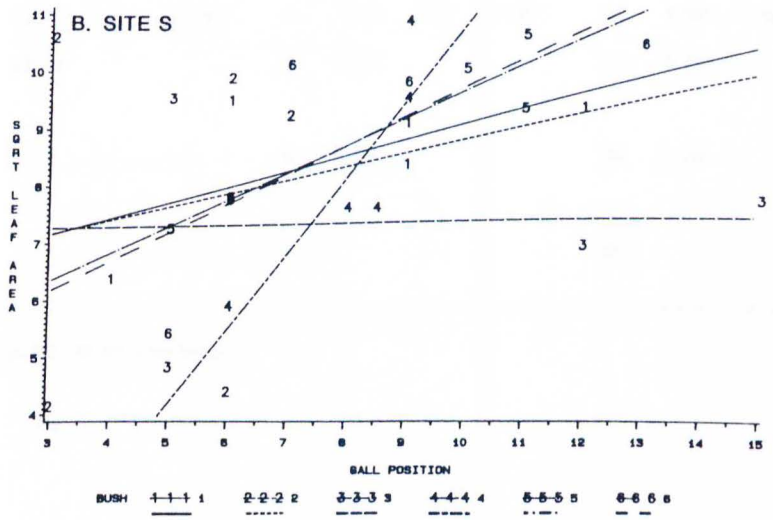
Table 4. ANCOVAs of leaf area and gall position (covariate) among replicate bushes during the period of asymptotic peak reproduction at highland sites G and S in July-August, 1986, and at lowland site P in May, 1986.

	Site G				Site S				Site P			
Source of Variation	df	MS	F	p	df	MS	F	p	df	MS	F	p
Date	3	66.29	0.64	.6 (NS)	-	-	-	-	2	541.50	2.54	.09 (NS)
Bush	5	1086.35	10.49	.0001***	5	180.87	0.49	.8 (NS)	4	546.11	2.56	.05*
Date*Bush	15	126.83	1.22	.2 (NS)	-	-	-	-	8	269.95	1.26	.3 (NS)
Gall Position	1	1740.48	16.80	.0001***	1	1471.56	3.98	.058 (NS)	1	2478.84	11.61	.001**
Error	95	103.59			22	490.12			48	213.58		
Total	119				28				63			

* $p<.05$, ** $p<.01$, *** $p<.001$, NS not significant.

Figure 2. The relationship of final leaf area (cm2) to position of the gall on the leaf among replicate bushes at A, highland site G, B, highland site S, and C, lowland site P.


A. SITE G
SQRT LEAF AREA
BALL POSITION


B. SITE S
SQRT LEAF AREA
BALL POSITION
BUSH 1 1 1 1 2 2 2 2 3 3 3 3 4 4 4 4 5 5 5 5 6 6 6 6

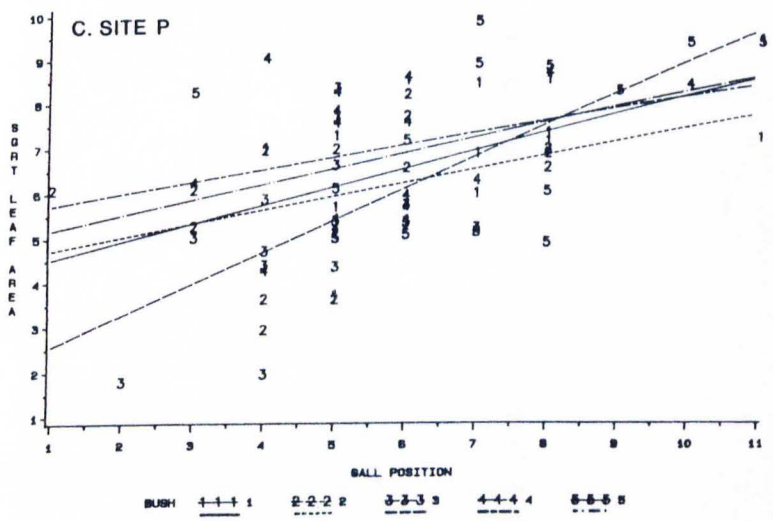

C. SITE P
SQRT LEAF AREA
BALL POSITION
BUSH 1 1 1 1 2 2 2 2 3 3 3 3 4 4 4 4 5 5 5 5

Table 5. Nested ANOVAs of gall density and the dependent variables leaf area, gall area, and fundatrix fecundity from one bush at site S during the 4-week period of asymptotic peak reproduction in July-August, 1985.

	Leaf Area				Gall Area				Fecundity			
Source of Variation	df	MS	F	p	df	MS	F	p	df	MS	F	p
Date	3	32.66	0.27	.85 (NS)	3	3.434	2.86	.048*	3	1.826	6.22	.002**
Density	4	406.05	3.32	.02*	4	5.569	4.63	.004**	4	1.201	4.09	.007**
Date*Density	12	123.51	1.01	.46 (NS)	12	2.032	1.69	.10 (NS)	12	0.430	1.46	.2 (NS)
Leaf(Date Dens) (Experimental Error)	42	122.18			42	1.203			42	0.294		
Gall(Leaf) (Sampling Error)	-	-	-	-	96	0.834			96	0.159		
Total	61				157				157			

* p<.05, ** p<.01, *** p<.001, NS not significant.

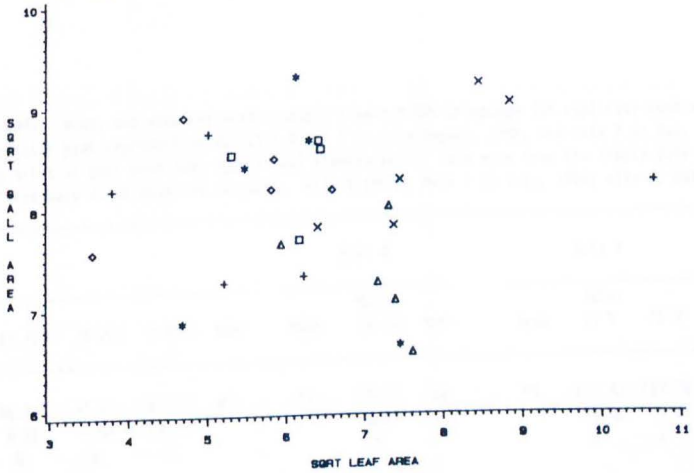
Table 6. Correlation analysis of leaf area with gall area, and fecundity with gall area, during the period of asymptotic peak reproduction at sites G and S in July-August 1986, and site P in May 1986. r=Pearson's correlation coefficient, p=significance, N=sample size.

	Site G				Site S	Site P		
Date:	11 VII	17 VII	25 VII	2 VIII	25 VII	16 V	22 V	28 V
A. Leaf Area x Gall Area:								
r:	.081	.150	-.210	.063	.123	-.330	.064	-.260
p:	.67 (NS)	.43 (NS)	.91 (NS)	.74 (NS)	.53 (NS)	.14 (NS)	.76 (NS)	.31 (NS)
N:	30	30	30	30	29	22	25	17
B. Fecundity x Gall Area:								
r:	.642	.630	.724	.712	.559	.463	.544	.510
p:	.0001***	.0002***	.0001***	.0001***	.002**	.03*	.006**	.04*
N:	30	30	30	30	29	22	25	17

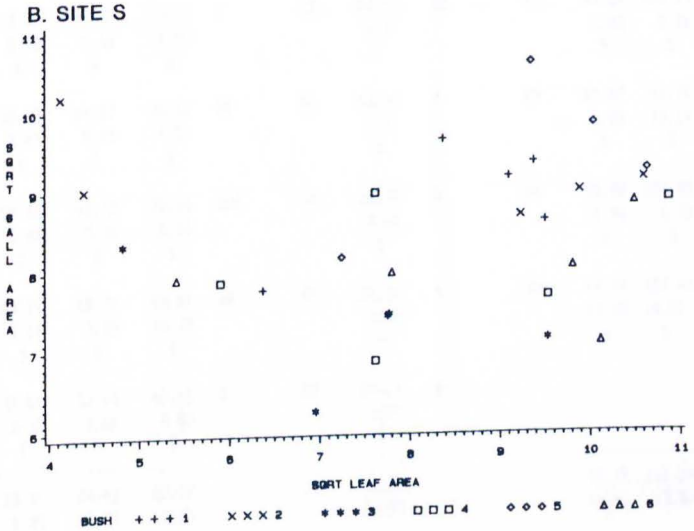
* p<.05, ** p<.01, *** p<.0001, NS not significant.

Figure 3. The relationship of gall area (mm2) to final leaf area (cm2) among replicate bushes at A, highland site G, B, highland site S, and C, lowland site P.

A. SITE G



B. SITE S



C. SITE P

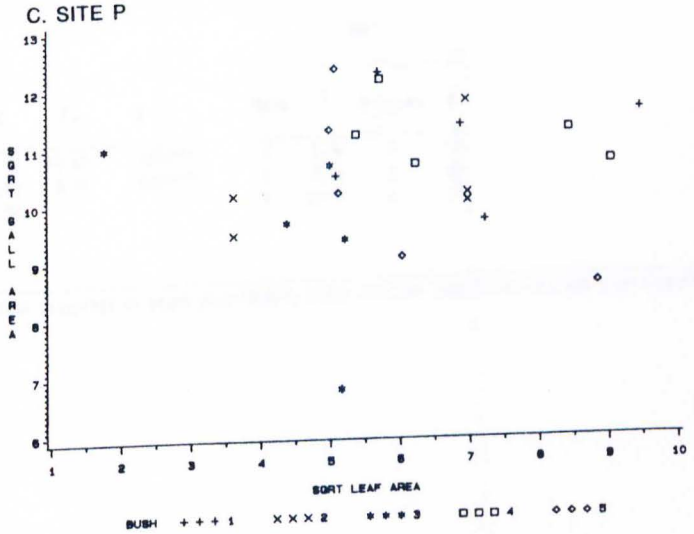


Table 7. A. Gall area (mm^2): mean, one standard error, sample size and SNK groupings for replicate bushes during the period of asymptotic peak reproduction at sites G and S in July-August, 1986, and site P in May, 1986.
B. ANOVA among sites of gall area (mm; square-root transformed). Data were from the sample date at each site when mature alates were first observed in galls. Site G and S, date = 25 July, 1986; site P, date = 28 May, 1986.

A.

Site G							Site S			Site P				
		Date:						Date:			Date:			
Bush		11 VII	17 VII	25 VII	2 VIII	SNK[1]	Bush	25 VII	SNK[1]	Bush	16 V	22 V	28 V	SNK[1]
G1	$\bar{X}$:	55.90	56.24	63.42	67.13	BC	S1	78.85	AB	P1	110.43	122.70	124.25	A
	SE:	7.69	8.00	4.54	12.74			5.59			18.66	9.84	3.07	
	N	5	5	5	5			5			3	5	3	
G2	$\bar{X}$:	74.29	73.32	71.10	73.11	A	S2	84.33	AB	P2	95.89	106.33	99.89	AB
	SE:	2.14	5.96	5.06	3.97			5.07			7.05	8.26	7.66	
	N:	5	5	5	5			5			5	5	3	
G3	$\bar{X}$:	63.83	58.98	64.37	58.13	BC	S3	53.48	B	P3	82.87	91.78	135.76	AB
	SE:	5.63	2.47	8.20	4.51			4.91			6.05	13.14	11.10	
	N:	5	5	5	5			5			5	5	5	
G4	$\bar{X}$:	51.76	59.18	68.32	70.10	ABC	S4	64.75	B	P4	99.98	124.90	133.86	A
	SE:	3.80	9.44	3.24	8.21			6.24			6.94	6.10	13.71	
	N:	5	5	5	5			5			4	5	3	
G5	$\bar{X}$:	71.68	63.71	68.25	68.81	AB	S5	89.32	A	P5	74.71	107.00	79.72	B
	SE:	3.40	2.61	3.59	10.79			9.50			12.05	14.54	4.66	
	N:	5	5	5	5			4			5	5	3	
G6	$\bar{X}$:	56.69	45.60	53.40	67.16	C	S6	63.11	B					
	SE:	2.38	3.16	3.60	4.59			4.42						
	N:	5	5	5	5			5						
Total	$\bar{X}$:	62.36	59.51	64.81	67.41			72.31			92.78	110.54	114.70	
	SE:	9.14	9.09	6.26	5.06			13.95			14.12	13.57	24.21	

B.

Source of Variation	df	MS	F_s	p
Site	2	37.87	65.62	.0001***
Bush(Site)	14	2.73	4.73	.0001***
Error	59	.58		
Total	75			

SNK[1]

Site	$\bar{X}$	Grouping	N
G	8.02	B	30
S	8.41	B	29
P	10.75	A	17

[1]Student-Newman-Keuls test groupings of means post-ANCOVA; means with the same letter are not significantly different; A>B>C.

Table 8. ANCOVAs of gall area and gall position (covariate) among replicate bushes during the period of asymptotic peak reproduction at highland sites G and S in July-August, 1986, and at lowland site P in May, 1986.

	Site G				Site S				Site P			
Source of Variation	df	MS	F	p	df	MS	F	p	df	MS	F	p
Date	3	1.229	1.57	.2 (NS)	-	-	-	-	2	6.623	6.79	.003**
Bush	5	3.157	4.03	.002**	5	3.362	5.71	.0016**	4	5.554	0.05	.0008***
Date*Bush	15	0.596	.76	.7 (NS)	-	-	-	-	8	2.348	2.41	.03*
Gall Position	1	0.871	1.11	.3 (NS)	1	.606	1.03	.3 (NS)	1	7.494	7.68	.008**
Error	95	0.782			22	.589			48	46.825		
Total	119				28				63			

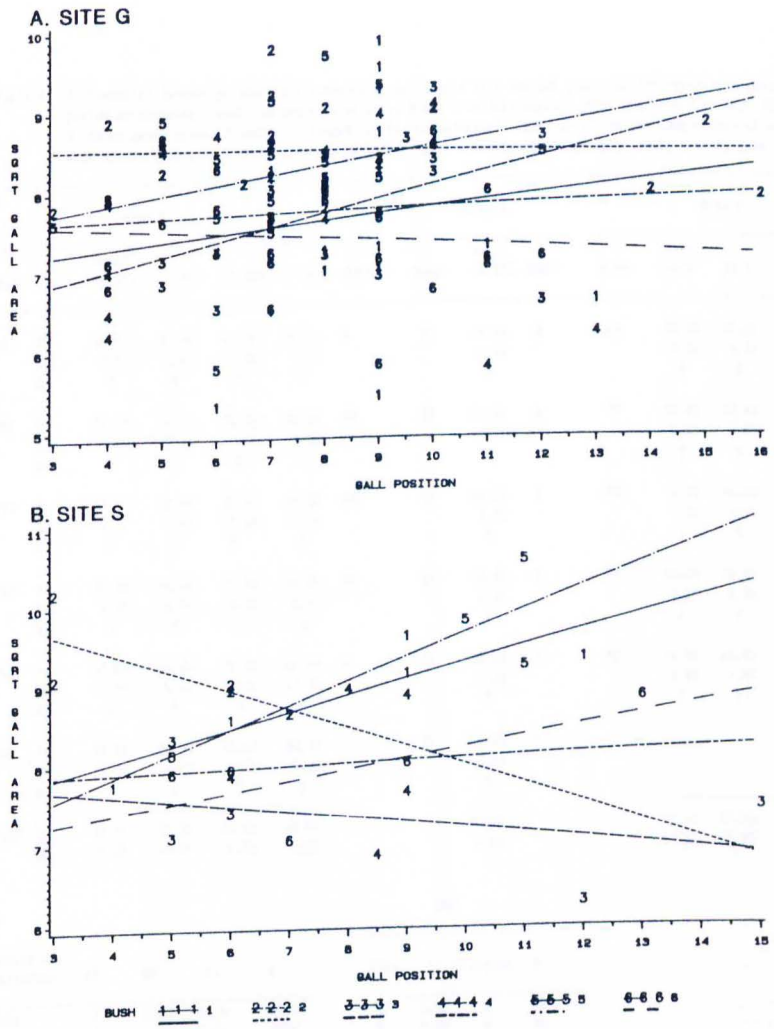
* p<.05, ** p<.01, *** p<.001, NS not significant.

at different rates (Table 8). At the two highland sites G and S, gall position did not contribute significantly to the variance in gall area (Table 8; Figure 4a, b). However, at lowland site P the effect of gall position on gall area was highly significant (Table 8) and negative: galls tended to be larger nearer the petiole (Figure 4c). Gall size was affected negatively by gall density per leaf at site S (Tables 2c, 5), but multiple comparison of means indicated that gall size at only the extreme densities of 1 and 16 were significantly different from each other (GT2; Table 2c).

Maximum fundatrix reproduction was significantly greater at the lowland site P than at the two highland sites G and S (Table 9). The numbers of second generation progeny in galls increased over sample dates at sites G and P (Tables 9a, 10, 11). The fecundity of fundatrices also varied significantly among bushes at highland site G and lowland site P (Tables 10, 11), but a significant date*bush interaction at site P indicated that aphids on different bushes were reproducing at different rates (Tables 10, 11). In curious contrast, fundatrix reproduction did not vary among bushes at site S (Table 10, 11). Analyses of covariance indicated that neither gall position (Table 10) nor final leaf area (Table 11) contributed significantly to the variance in fecundity at any site (Figures 5 and 6).

The correlation between gall area and fecundity was highly significant and positive on all 4 sample dates at

Figure 4. The relationship of gall area (mm2) to gall position among replicate bushes at A, highland site G, B, highland site S, and C, lowland site P.


A. SITE G
SQRT GALL AREA
BALL POSITION
B. SITE S
SQRT GALL AREA
BALL POSITION
BUSH 1 2 3 4 5 6

C. SITE P

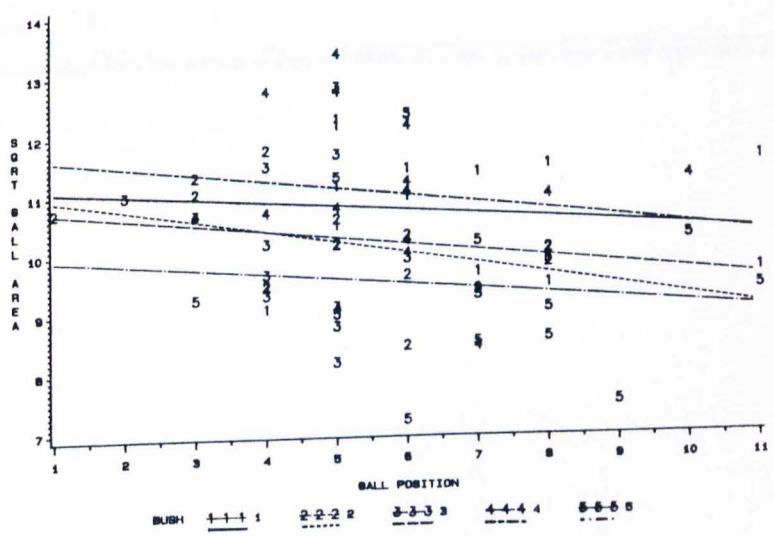

SQRT GALL AREA
BALL POSITION
BUSH 1 2 3 4 5 6

Table 9. A. Fundatrix fecundity: mean, one standard error, sample size and SNK groupings for replicate bushes during the period of asymptotic peak reproduction at sites G and S in July-August, 1986, and site P in May, 1986.
B. ANOVA among sites of fundatrix fecundity (log-transformed). Data were from the sample date at each site when mature alates were first observed in galls. Site G and S, date = 25 July, 1986; site P, date = 28 May, 1986.

A.

		Site G					Site S			Site P			
		Date:					Date:			Date:			
Bush		11 VII	17 VII	25 VII	2 VIII	SNK[1]	Bush	25 VII	SNK[1]	Bush	16 V	22 V	28 V	SNK[1]
G1	$\bar{X}$:	35.80	37.00	61.00	47.20	B	S1	50.60	A	P1	35.00	65.60	132.00	A
	SE:	4.91	5.62	4.38	9.24			5.80			9.54	9.24	11.90	
	N:	5	5	5	5			5			3	5	3	
G2	$\bar{X}$:	46.40	56.60	56.00	56.00	AB	S2	54.40	A	P2	20.00	75.40	113.00	AB
	SE:	3.93	3.66	6.14	6.57			4.27			2.37	8.99	12.06	
	N:	5	5	5	5			5			5	5	3	
G3	$\bar{X}$:	43.60	48.80	58.00	44.80	ABC	S3	44.20	A	P3	4.20	44.40	103.00	B
	SE:	4.32	4.52	11.40	6.01			4.75			.97	7.65	4.82	
	N:	5	5	5	5			5			5	5	5	
G4	$\bar{X}$:	36.80	45.60	57.40	46.80	BC	S4	53.40	A	P4	13.00	70.00	99.67	B
	SE:	4.43	8.43	5.05	8.64			6.42			2.89	4.29	16.13	
	N:	5	5	5	5			4			4	5	3	
G5	$\bar{X}$:	52.80	66.20	70.40	65.60	A	S5	58.50	A	P5	16.00	60.40	78.00	C
	SE:	3.57	6.19	8.16	12.75			6.02			3.00	7.87	10.00	
	N:	5	5	5	5			5			5	5	3	
G6	$\bar{X}$:	39.20	45.40	35.60	38.20	C	S6	54.00	A					
	SE:	5.99	4.89	4.24	8.97			5.44						
	N:	5	5	5	5			5						
Total	$\bar{X}$:	42.20	49.93	56.40	49.77			52.52			17.64	63.16	105.13	
	SE:	7.23	10.17	11.43	9.63			4.80			11.31	11.85	19.71	

B.

Source of Variation	df	MS	F_s	p
Site	2	2.850	45.15	.0001*
Bush(Site)	14	.146	2.31	.01**
Error	59	.063		
Total	75			

SNK[1]

Site	$\bar{X}$	Grouping	N
G	3.98	B	30
S	3.93	B	29
P	4.63	A	17

[1]Student-Newman-Keuls test groupings of means post-ANCOVA; means with the same letter are not significantly different; A>B>C.

Table 10. ANCOVAs of fundatrix fecundity and gall position (covariate) among replicate bushes during the period of asymptotic peak reproduction at highland sites G and S in July-August, 1986, and at lowland site P in May, 1986.

	Site G				Site S				Site P			
Source of Variation	df	MS	F	p	df	MS	F	p	df	MS	F	p
Date	3	.394	3.07	.03*	-	-	-	-	2	22.313	147.26	.0001***
Bush	5	.667	5.20	.0003***	5	.052	.89	.5 (NS)	4	1.753	11.57	.0001***
Date*Bush	15	.080	0.62	.9 (NS)	-	-	-	-	8	.817	5.39	.0001***
Gall Position	1	.113	.88	.4 (NS)	1	.064	1.11	.3 (NS)	1	.174	1.15	.3 (NS)
Error	95	.128			22	.058			48	.152		
Total	119				28				63			

* p<.05, ** p<.01, *** p<.001, NS not significant.

Table 11. ANCOVAs of fundatrix fecundity and leaf area (covariate) among replicate bushes during the period of asymptotic peak reproduction at highland sites G and S in July-August, 1986, and at lowland site P in May, 1986.

Source of Variation	Site G				Site S				Site P			
	df	MS	F	p	df	MS	F	p	df	MS	F	p
Date	3	.415	3.24	.03*	-	-	-	-	2	21.322	138.53	.0001***
Bush	5	.670	5.23	.0003***	5	.040	.66	.7 (NS)	4	1.680	10.91	.0001***
Date*Bush	15	.090	0.70	.8 (NS)	-	-	-	-	8	.702	4.56	.0004***
Leaf Area	1	.133	1.40	.3 (NS)	1	.008	.12	.7 (NS)	1	.053	.35	.5 (NS)
Error	95	.128			22	.060			48	.154		
Total	119				28				63			

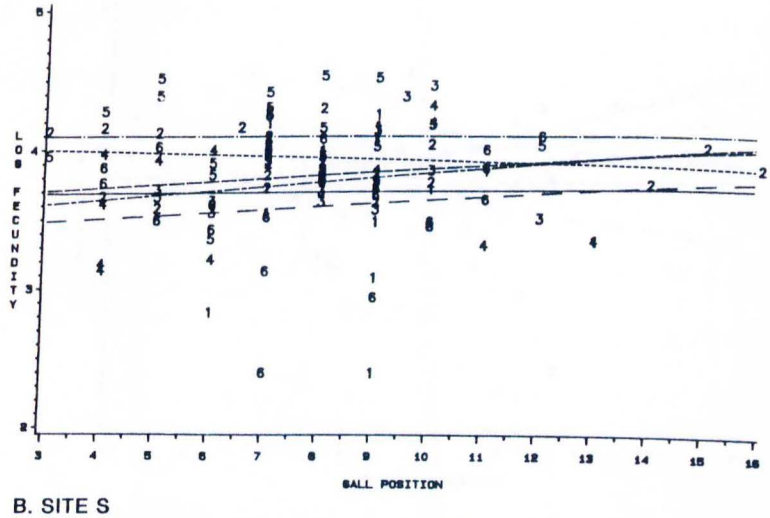
* p<.05, ** p<.01, *** p<.001, NS not significant.

Figure 5. The relationship of fundatrix fecundity to gall position among replicate bushes at A, highland site G, B, highland site S, and C, lowland site P.

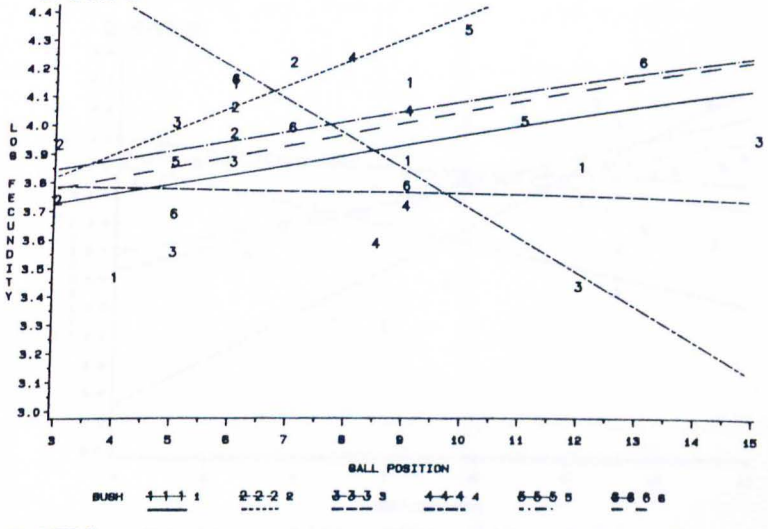
Figure 6. The relationship of fundatrix fecundity to final leaf area (cm2) among replicate bushes at A, highland site G, B, highland site S, and C, lowland site P.

Figure 7. The relationship of fundatrix fecundity to gall area (mm2) among replicate bushes at A, highland site G, B, highland site S, and C, lowland site P.

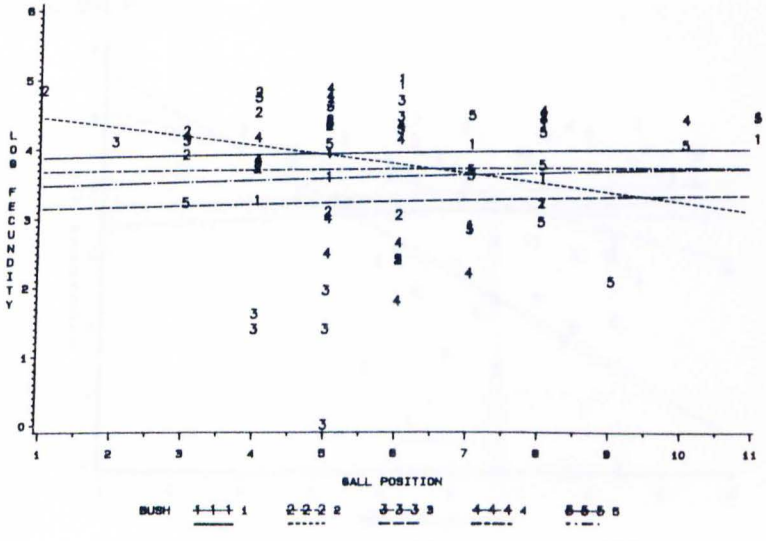
A. SITE G



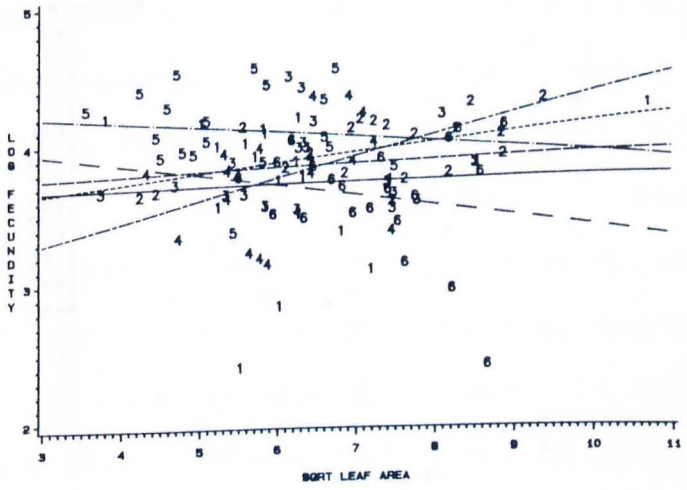
B. SITE S



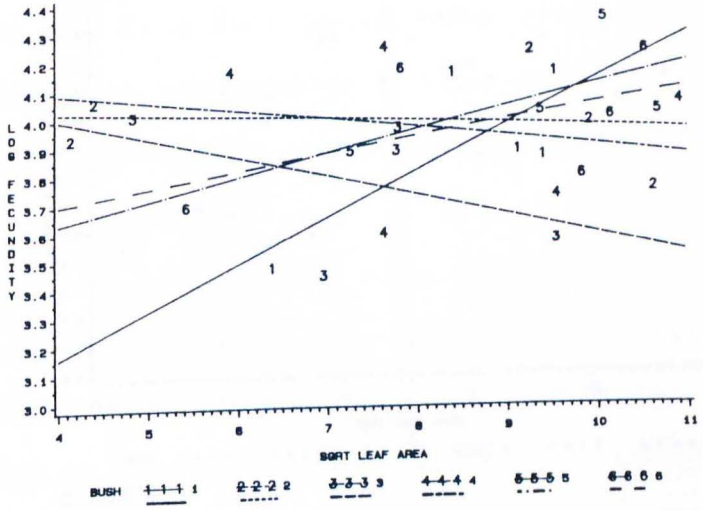
C. SITE P



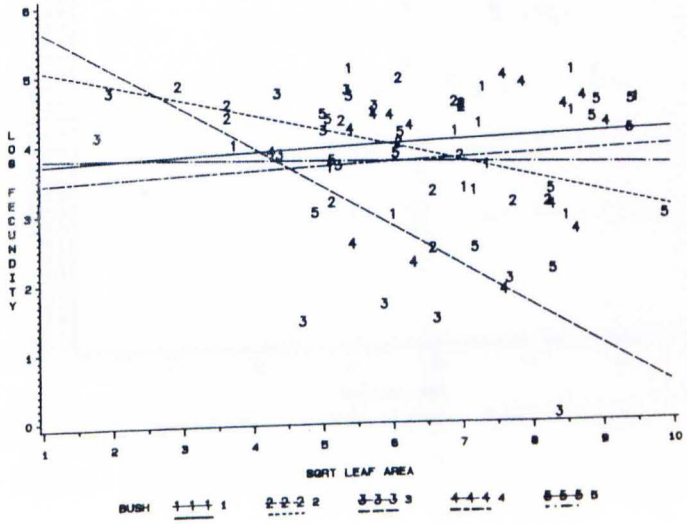
A. SITE G

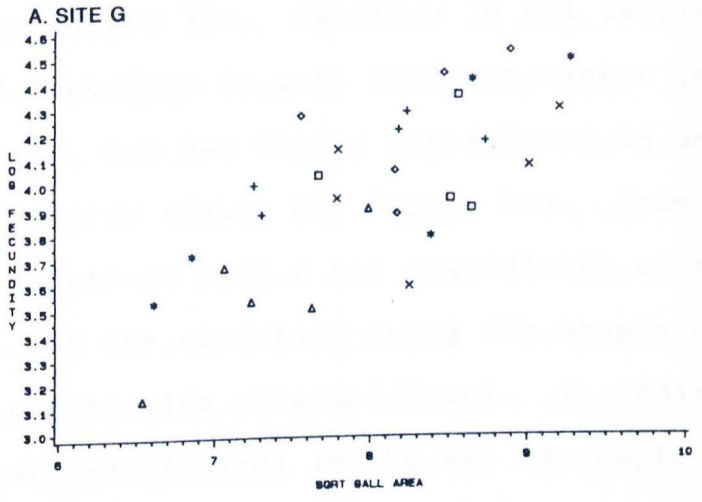


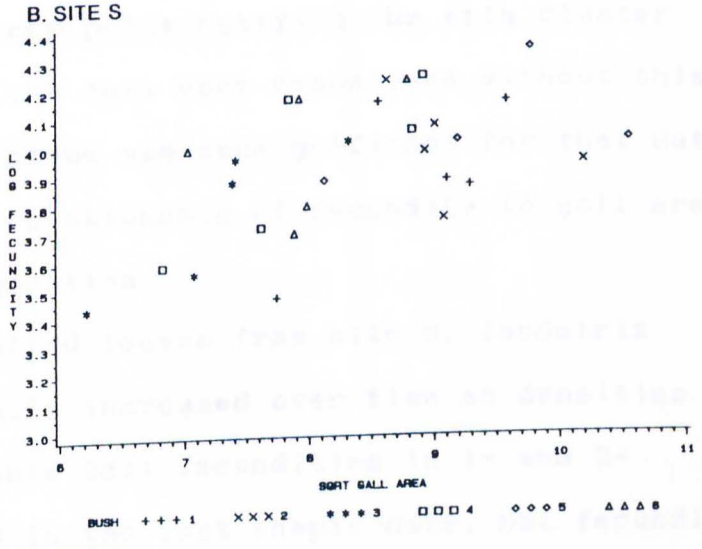
B. SITE S

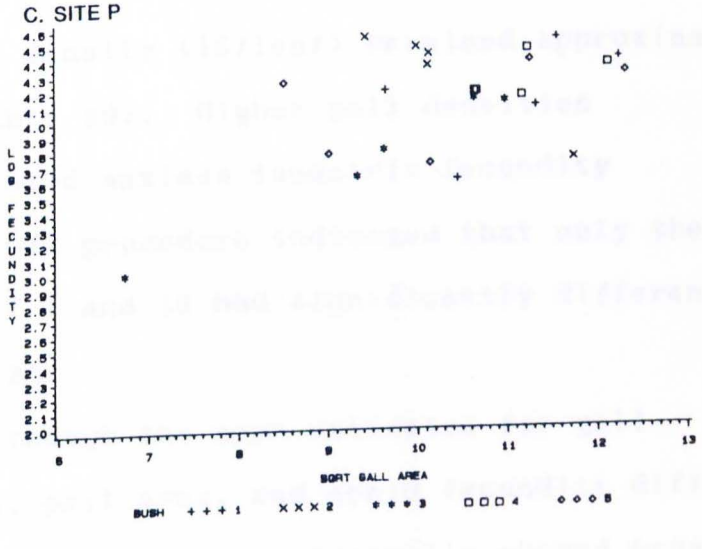


C. SITE P




A. SITE G
LOG FECUNDITY
SQRT GALL AREA


B. SITE S
LOG FECUNDITY
SQRT GALL AREA
BUSH + + + 1 × × × 2 * * * 3 □ □ □ 4 ◇ ◇ ◇ 5 △ △ △ 6


C. SITE P
LOG FECUNDITY
SQRT GALL AREA
BUSH + + + 1 × × × 2 * * * 3 □ □ □ 4 ◇ ◇ ◇ 5

site G (Table 6b; Figure 7a), and on the single sample date at site S (Table 6b; Figure 7b). Positive in all samples, the relationship of fecundity to gall area was weaker in 2 sample dates at site P, but was highly significant in one date (May 22) at that site (Table 6b, Figure 7c). Each of the correlations per date at site P was significant at the .05 level or lower, but the variation among the sample dates rendered the total correlation nonsignificant. In addition, most of the weight of significance in the May 22 sample date appeared to lie in one point outlying the main cluster (Figure 7c). When the data were reanalyzed without this outlier, the correlation was nonsignificant for that date ($p > .22$). Thus the relationship of fecundity to gall area at site P remains in question.

On multiple-galled leaves from site S, fundatrix reproduction generally increased over time at densities of 1 to 8 galls/leaf (Table 2d); fecundities in 1- and 2-galls/leaf declined in the last sample date, but fecundities in the highest gall density (16/leaf) remained approximately equal over time (Table 2d). Higher gall densities significantly depressed maximum fundatrix fecundity (Table 5), but the GT2 procedure indicated that only the extreme densities of 1 and 16 had significantly different fecundities (Table 2d).

In summary, although the mean estimates for gall position, leaf area, gall area, and aphid fecundity differed among the 3 sites, these locations generally showed broad

agreement in the relationships among the 4 variables. Galls were larger and aphids more fecund in the lowlands than the highlands. Leaves were largest at one highland site; galls grew larger at basal leaf positions in the lowlands but not in the highlands. Galls at the base of leaves depressed leaf area at sites G and P. Fecundity and gall area were positively correlated at sites G and S, but probably not at site P. Examined at site S only, gall density negatively affected gall area, leaf area, and fundatrix fecundity. No other significant relationships were discerned.

DISCUSSION

In contrast to Whitham's (1978, 1979, 1980, 1986) findings on the interaction of P. betae aphids with cottonwoods, the most striking features of Hormaphis leaf gall aphids on witch-hazel were the absence of effects of leaf size and gall position on aphid reproduction. That no aggressive or territorial behaviors were observed in Hormaphis is consistent with this result. The fact that proximal and distal positions on a leaf, and leaves of all sizes are equally suitable to these aphids suggests that quality resources are unlimited for H. hamamelidis aphids. Hence there is no density-dependent stress in this system that would promote the type of resourse-based territorial behavior evident in the Pemphigus-cottonwood system.

These results are not altogether unexpected, given the differences in the biology of hormaphidine and pemphigine aphids. Pemphigus aphids create large, elongate galls that extend along the leaf midrib (Whitham, 1986); the fact that each fundatrix produces 300 or more offspring (Whitham 1978, 1986) suggests that the nutrients appropriated by each gall must be great. Pemphigus reproductive success is therefore critically dependent upon the position of the gall on the leaf (Whitham 1986) presumably because interception of nutrient flow to the leaf tissue is greatest near the petiole (Whitham 1983, 1986), and the concentration of allelochemicals is lowest at this site (Zucker 1982). In fact, there is only one optimal gall site for Pemphigus

aphids (Whitham 1978). In contrast, Hormaphis aphids form much smaller protruding cone-shaped galls that cover very small leaf surface areas and contain less tissue per supporting leaf tissue than do Pemphigus galls. Hormaphis galls may be found on major veins anywhere on the leaf surface and presumably have much smaller rates of nutrient flow to each gall. In addition, fecundity per gall is lower and therefore competition among adjacent galls is expected to be small. The smaller galls and fewer progeny of Hormaphis fundatrices may reduce the dependency on nutrient translocation, and thus on position within a leaf. It is also possible that Hamamelis leaves may not possess the within-leaf heterogeneity in allelochemistry characteristic of Populus leaves (Whitham 1983, 1986; Zucker 1982).

In constrast to the independence of aphid reproduction from leaf area and gall position, gall size is highly related to highland Hormaphis fecundity, as it is for Pemphigus aphids (Whitham, 1986). Because witch-hazel galls continue to grow throughout the period of aphid reproduction and development, some galls may grow larger because the collective feeding action of a fundatrix with a larger progeny may stimulate gall growth more intensely, perhaps through the injection of plant growth regulators or amino acids (Kennedy and Stroyan, 1959; Lewis and Walton, 1958; Mani, 1964; Miles, 1968), or by creating a nutrient "sink" (Way and Cammell 1970) that is beneficial to gall development as well as to aphids. In a reciprocal fashion,

the development of larger galls with more phloem tissue may enhance aphid fecundity through better nutrition and by mitigating the negative effects of crowding, which are known to affect free-living aphids (Dixon, 1966, 1970, 1979; Dixon and Glen, 1971; Dixon and Wratten, 1971; Dixon, Burns, and Wangboonkong, 1968).

Because mean gall areas and their accompanying fecundities were variable among bushes, there must be bush-dependent characteristics such as the concentration of nutrients or allelochemicals that affect gall size and aphid fecundity. Bush quality for aphids might also be a function of the timing of leaf expansion; individual witch-hazel bushes were variable in their dates of first bud break (personal observation). Because fundatrices hatch long before bud break, they are ready to initiate their galls at first leaf expansion. Bushes that leaf out earliest in the spring may provide a longer growing season for galls and aphids, and may allow fundatrices to mature and begin reproduction earlier. Thus, the largest galls and highest fecundities in each weekly sample might have been those from the earliest bushes to break bud. The exact dates of bud break for individual bushes were not recorded in this study, but are being investigated in ongoing projects.

The most important determinant of gall size is probably the gall-forming behavior of 1st instar fundatrices. The "stinging" action of the young fundatrix forms the circular shape of the gall at its base (Lewis and Walton, 1958).

These probings delimit the circumference of the early gall, and therefore probably affect the total size of the mature gall. Because gall width accounts for 64% of total surface area (r=.80, p=.0001 at site G; r=.85, p=.0001 at site P), the behavior of the fundatrix (in highland populations, at least) at the earliest stage of gall formation could determine a large proportion of her maximum future reproduction. This conclusion parallels that by Whitham (1986), who found that Pemphigus gall size was dependent upon the amplitude of the fundatrix's probing activities on developing leaves.

Genetically or environmentally induced differences in body size between lowland and highland fundatrices (mature lowland fundatrices are larger than highland ones (von Dohlen, personal observation), and presumably are also larger in the first instar) might influence the probing radius of the aphid, and thus the final gall size. Although plant genotype may interact with the behavioral and genetic characteristics of the gall-inducing agent and thus affect gall phenotype (Miles, 1968; Weis and Abrahamson, 1986), the observation that highland and lowland galls retain their distinctive sizes where they grow together on the same bushes (and on the same leaves) where both occur syncronically (site L, von Dohlen and Gill, MS) discounts any contribution of plant genotype to the variation in gall size. The larger size of lowland galls could also be a consequence of their more basal positions and rapid growth

during the brisk development of leaves and galls in early spring at that site. Faster-growing tissue is easier to gall, and leaves grow more rapidly at the base than at the tip (Dixon, 1985; Forrest and Dixon, 1975)

Even though lowland galls were significantly larger at positions proximal to the leaf petiole, aphid fecundity was not greater at those positions. This result reinforces the doubts raised about the correlation between fecundity and gall area at site P (see Results section), and suggests that Hormaphis reproduction in the lowlands is not ultimately limited by gall size, as is Pemphigus fecundity by even the largest host leaves available to them (Whitham, 1978). Highland fundatrices, on the other hand, might increase their reproductive output if they could form larger galls.

The positive relationship between gall position on a leaf and resulting leaf area could conceivably translate into a fitness cost to host witch-hazels, particularly in the lowland location. Galls initiated in the basal area of the leaf may divert proportionally more nutrients into their own growth, and away from the developing leaf tissue. Reductions in leaf area as a consequence of aphid infestation has been shown to decrease significantly the size of the annual growth ring in large trees (Dixon, 1971). Oddly, because gall area is not affected by position in the highlands, an assertion that basal galls depress leaf growth implies that at highland sites fewer nutrients are translocated to leaves with basal galls. If witch-hazels do

incur a cost from Hormaphis herbivory, it should be related to the proportion of galled leaves per bush, and the proportion of galls that are near the petiole. Observations suggest (D. Gill, personal communication) that the impact of Hormaphis on highland Hamamelis in years of aphid outbreak may be severe: entire witch-hazel ramets have died after 1-2 years of heavy infestation.

At low densities of Hormaphis galls, the most important variables affecting fundatrix fitness may be the qualities of individual aphids and their interactions with the host plant. Only at high densities (16 galls/leaf) do Hormaphis aphids begin to show signs of intraspecific competition for host resources through decreased gall size and reproduction. Perhaps because of their small size in relation to the host leaf, and the fact that they are not limited to the midrib vein, several Hormaphis galls may be supported by a leaf without incurring the negative consequences that Pemphigus aphids experience at densities as low as 2 galls/leaf (Whitham 1978, 1980, 1986). Insufficient sample sizes precluded statistical tests of the impact of gall position on reproduction at different gall densities. However, due to the overall absence of gall position effects on fecundity and the fact that the average position did not vary with density at site S, gall position within a leaf is not expected to influence reproduction at densities >1 gall/leaf. The consequences of high density on the more intense gall growth and aphid reproduction at the lowland

site remain to be studied (and may show differences from highland sites). Hormaphis densities substantially greater than the highest density considered in this analysis (>20 galls/leaf) were observed on rare leaves during the study and in earlier outbreak years (1979-1980; D. Gill, personal communication). Decreases in fecundity might be severely depressed at these extreme densities, and could have contributed to the population crash in the years (1981-present) following the outbreak.

This study was not able to address questions of how gall position, gall density, leaf size, or gall size might influence the developmental rate of alate progeny to maturity, as Whitham (1980) has done. One piece of evidence does suggest that alates may mature faster when only one or two galls occupy a leaf: the decline in aphids/gall in the two lowest densities of the last sample date (Table 2d) may have been due to the departure of alates that had matured earlier at the lower densities. Rapid development and abandonment of galls becomes important as the season progresses, particularly in the lowlands. Up to 70% of lowland galls were invaded in both 1985 and 1986 by coccinellid or syrphid larvae that consumed the entire contents of a gall before many of the alates could mature (von Dohlen and Gill, MS). Bird predation on galls in 1985 and 1986 occurred predictably at both highland and lowland sites just before alates began to depart from galls and when aphid density/gall was greatest (personal observation). The

first clones to mature alates and abandon their galls may have a greater probability of contributing larvae to the next generation on river birch.

SUMMARY

The relationships of the ecological variables of gall position, gall density, leaf size, gall size, and fecundity for the aphid Hormaphis hamamelidis have been found to differ greatly from those reported elsewhere for another aphid, Pemphigus betae (Whitham, 1978, 1979, 1980, 1986). While both aphids are similar in that fundatrices create galls on the leaves of their primary host plant in which they parthenogenetically produce an alate second generation, the factors affecting selection of gall sites and the effects of gall position and leaf area on gall size and aphid fecundity, and the interaction of density with all these factors, are very dissimilar. Whereas Pemphigus fundatrices competete aggressively for the best gall territories on a leaf and tolerate only low densities per leaf (≤ 4) (Whitham, 1979, 1980, 1986), Hormaphis are passive and nonterritorial and may reach densities higher than 20 galls/leaf. In contrast to the striking affects of leaf size and gall position on gall size and aphid reproduction for Pemphigus (Whitham, 1978, 1980), leaf area has no detectable impact on Hormaphis fecundity, and the positions of galls within leaves affects gall size in the lowlands only and fecundity not at all. The dynamics of Hormaphis reproduction are similar to Pemphigus in only two respects, namely, the influences of gall density (negative) on gall size and fundatrix fecundity, and the correlation of gall size (positive) with fecundity, although the consequences of

density for Hormaphis do not approach the extreme for Pemphigus.

The differences in biology between Hormaphis hamamelidis and Pemphigus betae and the qualities of their respective host plants most likely account for the observed departures in several features of their intraspecific and host-plant interactions. The fact that Hormaphis form smaller galls of a different shape and are less fecund may reduce their susceptibility to density effects and to within- and among-leaf microhabitat heterogeneity. As a host plant, witch-hazel may not present Hormaphis with the kinds of habitat limitations that are so critical to Pemphigus on cottonwood.

REFERENCES

Dixon, A.F.G. 1966. The effect of population density and nutritive status of the host on the summer reproductive activity of the sycamore aphid, Drepanosiphum platanoides (Schr.). Journal of Animal Ecology 35:105-112.

Dixon, A.F.G. 1970. Quality and availability of food for a sycamore aphid population. In A. Watson, ed., Animal Populations in Relation to their Food Resources. Symposia of the British Ecological Society 10:271-287.

Dixon, A.F.G. 1971. The role of aphids in wood formation. I. The effect of the sycamore aphid, Drepanosiphum platanoides (Schr.) (Aphididae), on the growth of sycamore, Acer pseudoplatanus (L.). Journal of Applied Ecology 8:165-179.

Dixon, A.F.G. 1979. Sycamore aphid numbers: The role of weather, host and aphid. pp. 105-131 in R.M. Anderson, B.D. Turner, and L.R. Taylor, eds., Population Dynamics. 20th Symposium British Ecological Society London. Blackwell Scientific Publishers, Oxford.

Dixon, A.F.G. 1985. Aphid Ecology. Blackie, Glasgow.

Dixon, A.F.G., and D.N. Glen, 1971. Morph determination in the bird cherry-oat aphid. Annals of Applied Biology 68:11-21.

Dixon, A.F.G., and S.D. Wratten. 1971. Laboratory studies on aggregation, size and fecundity in the black bean aphid, Aphis fabae Scop. Bulletin Entomological Research 61:97-111.

Dixon, A.F.G., M.D. Burns, and S. Wangboonkong. 1968. Migration in aphids: Response to current adversity. Nature 220:1337-1338.

Forrest, J.M.S., and A.F.G. Dixon. 1975. The induction of leaf roll galls by the apple aphids Dysaphis devecta and D. plantaginea. Annals of Applied Biology 81:281-288.

Kennedy, J.S., and H.L.G. Stroyan. 1959. Biology of aphids. Annual Review Entomology 4:139-160.

Lewis, I.F., and L. Walton. 1958. Gall formation on Hamamelis virginiana resulting from material injected by the aphid, Hormaphis hamamelidis (Fitch). Transactions American Microscopical Society.

Mani, M.S. 1964. The Ecology of Plant Galls. Monographiae Biologicae, vol. 12. Junk, The Hague.

Miles, P.W. 1968. Insect secretions in plants. Annual Review of Phytopathology 6:137-164.

Morgan, T.H., and A.F. Shull. 1910. The life cycle of Hormaphis hamamelidis. Annals Entomological Society America 3:144-146.

Pergande, T. 1901. The life history of two species of plant-lice inhabiting both the witch-hazel and birch. U.S. Department of Agriculture Technical Series 9:7-44. Government Printing Office, Washington, D.C.

Sokal, R.R., and F.J. Rohlf. 1981. Biometry. W.H. Freeman and Co., New York. 2nd Edition.

SASR User's Guide: Statistics, Version 5 Edition. 1985. SAS Institute, Cary, North Carolina.

von Dohlen, C.D. and D.E. Gill. Geographic variation and evolution in the life cycle of the witch-hazel leaf gall aphid, Hormaphis hamamelidis. (Manuscript in review)

Way, M.J. and M. Cammel. 1970. Aggregation behavior in relation to food utilization by aphids. In A. Watson ed., Animal Populations in Relation to their Food Resources. Symposia British Ecological Society 10:229-247.

Weis, A.E. and W.G. Abrahamson. 1986. Evolution of host manipulation by gall makers: Ecological and genetic factors in the Solidago-Eurosta system. American Naturalist 127:681-695.

Whitham, T.G. 1978. Habitat selection by Pemphigus aphids in response to resource limitation and competition. Ecology 59:1164-1176.

Whitham, T.G. 1979. Territorial behaviour of Pemphigus gall aphids. Nature 279:324-325.

Whitham, T.G. 1980. The theory of habitat selection: Examined and extended using Pemphigus aphids. American Naturalist 115:449-466.

Whitham, T.G. 1983. Host manipulation of parasites: Within-plant variation as a defense asgainst rapidly evolving pests. pp. 15-41 in R.F. Denno and M.S. McClure eds., Variable Plants and Herbivores in Natural and Managed Systems. Academic Press, New York.

Whitham, T.G. 1986. Costs and benefits of territoriality: Behavioral and reproductive release by competing aphids. Ecology 67:139-147.

Zucker, W.V. 1982. How aphids choose leaves: The roles of phenolics in host selection by a galling aphid. Ecology 63:972-981.