Variation in the Effects of Host Plant on the Pea Aphid, *Acyrthosiphon pisum* (Harris) (Homoptera: Aphididae)

by

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ABSTRACT

BY

S.M.C. Subasinghe

Variation in the effects of host plant on the pea aphid, Acyrthosiphon pisum (Harris) (Homoptera: Aphididae)

Field and laboratory studies were carried out on the variation in host plant responses of Acyrthosiphon pisum. The relationship between aphid response on previous host plant and responses to new host plants was also examined. Field transfers were made among plots of alfalfa, sainfoin, trefoil, sweet clover, field peas and fababeans. Parameters estimated were mean survival and mean fecundity. Detailed studies were carried out in the laboratory with field collected samples of clones from different hosts. In this case, nymphal survival and adult dry weight were measured in addition to the parameters mentioned above.

Among aphids in any single field, great variation in response was observed when aphids were exposed to different host plants. This variation was as great as that reported between biotypes having diverse geographic origin. Moreover, characteristics of aphid populations on different hosts were not distinct and persistent. Clones present on one particular host plant show some short term selection during summer when reproduction is parthenogenetic, presumably through differential survival reproduction, and/or migration. This is followed by genetic recombination during sexual reproduction in the fall resulting in a

different set of aphid genotypes. There is no relationship between responses of clones to different host plants in one year and their responses to the same host plants in another year. Therefore, biotypes are annual phenomena.

Samples of clones from older, geographically separated populations showed some differences. These differences may be attributed to spacial separation, the high selection pressures exerted by insecticides on one of the populations or to the different varieties of the host. Relative status of this variation of clones available from widely different geographic areas, particularly where anholocycle prevails, remains to be established.

Clones exhibiting variable characteristics are not mutually exclusive. Therefore, the system of nomenclature currently being employed seems inappropriate. It appears that the sympatric biotypes of A. pisum prevailing in any population represent fairly simple genetic variants. Therefore, identifying and naming or otherwise labelling of clones of A. pisum could lead to confusion as it may give a false impression of the biological status of the insect.

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CHAPTER I

INTRODUCTION

1. Distribution and Economic Importance of Acyrthosiphon pisum.

Acyrthosiphon pisum (Harris), which is found on every continent of the world (Hill 1975), is often called the pea aphid. This common name does not reflect the real situation because only a small proportion of the forms and sub-species united under this name colonize the pea plant, especially in Europe (Muller 1981).

A. pisum, first described in Great Britain in 1776 (Harper et al. 1978), was introduced into North America from Europe in infested clover and peas (Folsom 1909). It was unknown in North America before 1878 and appeared as a crop pest for the first time in 1899 (Davis 1915). In addition to the usual green form, red and yellow aphids are also known to occur. The aphid may seriously damage peas, alfalfa, vetch, and clovers (Harper and Kaldy 1982). Patch (1938) and Eastop (1971) list the known hosts.

The economic importance of aphids was outlined by Palmer (1952) and is expressed in several ways:

a. robbing of plant sap,

b. toxic action of salivary secretions, injected during feeding, and causing stunted growth, deformation of leaves or fruits, galls on leaves, stems or roots,

c. vectoring of virus diseases of plants,

d. deposition of honey-dew on plant surfaces.

The pea aphid usually infests the growing tips of plants. Both adult and young aphids pierce the plant tissue and suck juice from leaves, petioles, stems, and flower buds. Heavily infested plants become stunted and wilted, the top leaves turn light green, and the lower ones turn yellow and die. As a result, the yield and quality of the crop may be greatly reduced. In the United States, infestations of the pea aphid have been responsible for losses in alfalfa production of about $60 million a year (Carnahan et al. 1963). Control of pea aphids with insecticides has increased alfalfa hay yields up to 152% (Franklin 1953). A. pisum is also reported to reduce winter hardiness of alfalfa (Harper and Freyman 1979). The pea aphid has affected yield by significantly reducing the mean heights of alfalfa by 45%, the green weight by 38%, the dry weight by 44%, and the fiber by 13% (Harper and Kaldy 1982). Feeding by A. pisum on young pea plants in the laboratory reduced the relative growth rate and efficiency of production of new tissue relative to the amount of leaf area by as much as 118% (Barlow and Messmer 1982). Although the figures in the above two references are based on laboratory experiments, it illustrates the potential of A. pisum as a pest on cultivated legumes.

There are some 170 plant viruses transmitted by 102 species of aphids but some aphid species can transmit a large number of different viruses. For example, Myzus persicae (Sulz.) can transmit 108 different plant viruses (Lamb 1974). The pea aphid is also known to be a vector of plant diseases. The principal viruses it transmits are alfalfa mosaic, alsike clover mosaic, bean yellow mosaic, pea enation mosaic, pea mosaic, pea

streak, and red clover vein mosaic (Harper et al. 1978). On fababeans, virus diseases caused 59-96% reduction in yield (Frowd and Bernier 1977).

The pea aphid, A. pisum, occurs in synonymy in the literature under various scientific names including: Acyrthosiphon onobrychis, A. pisi, A. pisi destructer, A. pisi pisi, A. pisi turanicum, A. pisi ussurensis; Anuraphis (Macchiatiella) promedicagnis; Aphis pisi, A. lathyri, A. onobrychis, A. ulmariae; Illinoia pisi; Macchiatiella trifolii; Macrosiphum genistae, M. onobrychis, M. ononis, M. pisi, M. pisum, M. theobaldi, M. trifollii, M. ulmariae; Nectarophora pisi, N. destructor, N. pisi destructor; Siphonophora corydalis, S. ononis, S. Pisi, S. spartii, and S. ulmariae (Eastop 1971).

2. Purpose of the Study

There is some evidence that individual aphids are more restricted in their host-plant relationship than the species as a whole (e.g. Cartier 1959; Cartier et al. 1965; Frazer 1972). This restriction has led to the adoption of the concept of 'biotypes' in aphid biology. Although many studies have documented such variations among different clones of A. pisum, in most studies the variation among individuals within a population and that among populations has not been examined in detail. It also appears that some workers have used only a single clone and drawn conclusions made by ecologists in studying entire populations. Documentation of any intra-population as well as inter-population variation in host plant preferences would assist in describing the exact nature of this intra-specific variation and of resource utilization patterns, and would also be expected to provide some indication on shifts to new

host plants.

A feature of the life cycle of A. pisum in Manitoba is cyclical parthenogenesis in which a series of parthenogenetic generations in spring and summer are combined with a single annual sexual generation which entails genetic recombination. During the course of the season some of these new parthenogenetic clones will survive, while others may be eliminated. Those surviving clones will contribute to the gene pool for the next year's aphids. A knowledge of such intra-specific variation is of importance because 'biotypes' may be of very different economic importance as pests or as vectors of virus diseases and their existence renders the breeding of resistant plant varieties more difficult. In addition, the study of intra-specific variation is relevant to studies of mechanisms of host acceptability and host avoidance. Such research appears essential for the understanding of evolutionary processes, especially the evolution of resistance in insects (Bush 1975b).

The purpose of this project was to examine the variation in host-plant preferences of A. pisum. The experiments were designed in such a way as to achieve the following experimental objectives:

a. To determine the extent of variation in host-plant preferences among aphids available from populations infesting a single crop,

b. To determine the extent of variation in host-plant preferences between crops,

c. To examine changes over the season in the extent of variation in host-plant preferences on a crop.

Achievement of the above objectives might be expected to provide data to distinguish whether biotypes are distinct and persistent genetic strains adapted to a given host plant (perennial), or seasonal phenomena caused by annual cycles of sexual reproduction (annual).

3. Definitions of Terms Used

Anholocyclic - Not capable of reproducing via hibernating eggs, therefore not capable of producing sexuals or viable eggs.

Clone - the individuals of successive parthenogenetic generations which are the offspring of a single fundatrix and therefore possess the same genotype as their stem mother which developed from a fertilized egg.

Fundatrix (stem mother) - viviparous parthenogenetic female developing from a fertilized egg.

Holocyclic - capable of producing sexuparae, sexuals and fertilized eggs and therefore there is an interruption of the thelytokous parthenogenetic reproduction.

Monophagous - aphids living on one host species only.

Nymphal development - the time taken for progeny to develop from birth to the adult stage.

Oligophagous - aphids living on few host species.

Popyphagous - aphids living on many host species.

Population	-	aphids existing on a particular host in a particular locality.
Primary host	-	a host on which the sexual cycle takes place.
Secondary host	-	a host on which only parthenogenetic reproduction takes place.
Sexuals	-	males and gamic females. The females mate with the males and lay fertilized eggs.
Sexuparae	-	individuals which give birth to both sexes of the gamic stage in the cycle.
Thelytoky	-	parthenogenetic development in which only females are produced.
Virginopara	-	viviparous parthenogenetic female producing other parthenogenetic viviparae.

CHAPTER II

LITERATURE REVIEW

Much has been written concerning the intraspecific variation in host plant relationship of insects which leads to the concept of biotypes in insect biology. An attempt will be made to bring together major references to such intraspecific variation with special reference to aphids so as to illustrate the extent of variation exhibited by such individuals having diverse geographic origins. In addition, a brief review will be presented on food selection by phytophagous insects with regard to different theories proposed and various factors that govern insect-plant relationships. Literature pertaining to life history and biology of A. pisum will also be dealt with.

1. Food Selection by Phytophagous Insects

Phytophagous insects show various degrees of specificity to plants (Dethier 1947, 1966; Beck 1974). They are polyphagous, oligophagous, or monophagous, depending on whether they feed on many, a few, or a single species of plant respectively.

The chemical composition of plants is of fundamental importance in their acceptance or rejection as food by insects. This probably is true with regard both to selection between different plant species (Nayar and Thorsteinson 1963; Hsiao and Fraenkel 1968), and to selection between different parts of a plant (Rees 1969). A food plant is characterized not only by the presence of specific chemical attractants or feeding stimulants called phagostimulants but also by the absence of

repellent secondary plant substances (Dethier 1954; Fraenkel 1969). The basic behavioural and physiological processes mediated by these compounds are host finding by adult females for feeding and oviposition, and host finding by immature stages for feeding, growth and development.

Two theories have been proposed to describe host plant selection by insects. One of the theories (Painter 1951, 1958; Thorsteinson 1960; Kennedy 1965) claims that the choice of food plants is governed by primary chemicals in the plant. Primary chemicals are defined as being that set of chemicals which are indispensable to the metabolic and developmental process of the insect (Beck 1974). They include various amino acids, lipids, carbohydrates, vitamins and minerals.

The second theory of food selection states that secondary plant chemicals are responsible for host plant selection by phytophagous insects (Dethier 1954, 1970; Fraenkel 1959, 1969; Schoonhoven 1972). Secondary plant chemicals are defined as non-nutrients usually elaborated as by-products of metabolic systems in the plant (Whittaker 1970; Whittaker and Feeny 1971). They are characteristically toxic, unpalatable, or offensive to non-adapted insects. They include glucosinolates, cucurbitacins and essential oils. This theory implies that the majority of host plants are nutritionally adequate for phytophagous insects and that host plant selection is based on the presence or absence of secondary plant chemicals.

It has also been recognized that both primary and secondary plant chemicals jointly are involved in host plant selection (Hsiao 1972; Beck 1974; Dethier 1976). Two or more primary chemicals may jointly

exert synergistic effects to incite an insect to feed. The effect of a secondary plant chemical as a feeding stimulant may be enhanced in the presence of a primary chemical. Both primary and secondary chemicals can also act jointly to inhibit feeding. Dethier (1976) concluded that although a particular compound or category of compounds may be the major chemical constituent of a plant and may contribute the major sensory cue, it is the total chemical complex of the plant that forms the basis of selection.

Studies of insect-plant interactions have led to some general conclusions: (a) insect feeding, development and survival are often inhibited by host plant defenses (Cates 1980; Haukioja 1980; Mattson 1980), (b) insect herbivores change plant competitive relationships through selective herbivory, (Connell and Slatyer 1977; Schowalter et al. 1981a), and (c) insect herbivores influence the rate and direction of nutrient transfer between vegetation and litter (Springett 1978; Schowalter et al. 1981b).

An acceptable host plant must provide the insect with a suitable environment and a nutritional substrate that is adequate, non-toxic, and utilizable. Beck (1974) pointed out that even the best host plants may be suboptimal in some of these characteristics and that mortality among larvae tends to be very high. The phenols, flavonoids, alkaloids and various glycosides contained in plants are deleterious and insects feeding on plants containing these substances must be able to degrade them metabolically (Beck 1965). The ability to metabolize such plant components constitutes an important aspect of the adaptation of an insect species to a particular plant as a host (Self et al. 1964;

Krieger et al. 1971). Different plant species may differ either qualitatively or quantitatively in respect to these substances. Therefore, an insect that is metabolically adapted to one type of plant may not be able to meet the metabolic demands posed by another plant. Consequently, the insect will not be able to survive on it.

There are several factors which govern insect-plant relationships. Among them, physical characteristics, bio-chemical characteristics, and nutritional factors are the most important. Since plants differ in these basic factors, most insects can only feed on a few selected food plants which allow optimal development and survival.

i. Physical characteristics

The role of physical characteristics has been studied mainly in relation to host plant resistance. Characteristics such as pubescence, spacing of vascular bundles and tissue silica content have been investigated.

Leaves with hairy surfaces may reduce feeding, increase mortality and depress growth in some phytophagous insects (Levin 1973; Wellso 1973), but not in some others (Maxwell and Jennings 1980). Hairy surfaces sometimes prevent insects from coming in contact with the leaf cuticle, thus acting as a physical obstruction to feeding. For aphids, a sticky substance discharged from glandular hairs on the leaves of several Solanum spp. entraps the insects and prevents their establishment (Gibson 1971). Gilbert (1971) reported that small caterpillars of Heliconiine butterflies are entrapped and effectively prevented from feeding by hook-like trichomes on the leaves of Passiflora adenopoda D.C. Young larvae of

Prodenia eridania (Cramer) are trapped and injured by fish-hook like spines on Dorsternia contrajerva L. (Soo Hoo and Fraenkel 1966). Physical characteristics may therefore either injure the insect directly or prevent it from feeding.

ii. Bio-chemical characteristics

It is commonly known that chemical stimuli play an important role in the feeding behaviour of many phytophagous insects. Secondary plant substances guide the insect's choice of food. A non-food plant is characterized not only by the absence of specific chemical attractants or feeding stimulants, but also by the presence of other secondary plant substances which act as repellents (Dethier 1954; Fraenkel 1969). These compounds together with nutrients account for insect-plant interactions.

Alfalfa is known to contain feeding stimulants for the alfalfa weevil, Hypera postica (Gryllenhull) (Yamamoto 1963). Hsiao (1969) reported that these compounds are adenine salts and nucleotides. Tannic acid in alfalfa acts as a repellent for alfalfa weevil larvae (Bennett 1965). The saponins in alfalfa have been indicated as a possible resistance factor not only to white grubs, Melolontha vulgaris F. (Horber 1965) but also to stored product insects in legume seeds (Applebaum et al. 1969).

Beans, Phaseolus spp., have been shown to contain feeding stimulants, phaseolunatim and lautaustrin, for the Mexican bean beetle, Epilachna varivestris (Mulsant) (Klingenburg and Bucher 1960). Sweet clover, Melitolus officinalis L., and other clovers contain coumarin, which is a feeding attractant for the vegetable weevil, Listroderes

costrirustris (Klug), at low concentrations but a deterrent in higher concentrations (Matsumoto 1962). Chlorogenic acid and rutin, major phenolic constituents of tomato foliage, inhibit growth of the fruitworm Heliothis zea Boddie larvae (Elliger et al. 1981; Isman and Duffey 1982), but rutin is reported to increase growth and fecundity of the larvae of Acheta domesticus (L.) (McFarlane and Distler 1982).

Variability in concentration of secondary substances may influence the feeding activity and developmental success of the insect. Colorado potato beetle larvae, Leptinotarsa decemlineata (Say), were observed to feed more readily and to grow better when fed young potato foliage than when given older tissues, while senescent foliage of either potato or tomato tended to retard growth (Bongers 1970; Cibula et al. 1967). Feeny (1968) showed that larvae of the winter moth, Operophtera brumuta (L.) consumed oak leaves early in the growing season, but not later, apparently because of a high concentration of tannins in older leaves. However, Bernays (1981) reported that though tannins do affect the growth and survival of insects, there is no unequivocal proof of an antidigestive effect of tannic acid or condensed tannin in insects. These results indicate that synchronization is an important factor in insect-plant relationships. Other researchers have emphasized the importance of proper synchronization between insect and host phenology for the development of most phytophagous insects (Embree 1965; Eidt and Little 1968).

iii. Nutritional requirements

It is generally accepted that the nutrient level and nutrient balance of a food plant will determine its adequacy for an insect. House

(1969) reported that for Celerio euphorbiae L., the amount of food eaten was greater when there was favourable nutrient balance. Altering the nutrient balance resulted in lower food consumption and a reduced efficiency of conversion from 20% on a normal balanced diet to 9.5% on an imbalanced diet.

Banks (1965) states that the fecundity of Aphis fabae Scop. seems to depend primarily on the quality of the nutrients it gets from its hosts. Auclair et al. (1957) and Maltais and Auclair (1962) found resistance of varieties of peas to A. pisum to be correlated with the relative concentrations of amino acids and glucose. The susceptible varieties generally contained a higher concentration of free and total amino acids than the resistant ones. According to Auclair (1963), asparagine, glutamine and homoserine are the factors determining the resistance of pea varieties. Some workers (Blais 1952; Wilde et al. 1969) have reported differences in nutrient content of plant structures of different ages and their apparent effects on insect growth, survival, and reproduction. Others (House 1969, 1970, 1971; Maltais and Auclair 1962; McGinnis and Kasting 1961) have suggested that dietary proportions of required nutrients may be of greater importance than their absolute quantities in food selection. Diets which lack one or more primary chemicals or have unsatisfactory ratios of these chemicals may be less acceptable to an insect.

The concentrations of some elements and minerals have been shown to have direct or indirect effects on the feeding behaviour and survival of insects. Allen and Selman (1957), working with Pieris brassicae

(L.), reported that deficiency of nitrogen and iron in a food plant caused a reduction in the relative growth rate of larvae and increased larval mortality.

Water, although not usually classified as a nutrient, may be an important factor to plant-feeding insects. Lepidopterous larvae generally maintain a body water content of 85-92% (Evans 1939; Wigglesworth 1975). The possible effects of plant tissue water content were considered by Waldbuer (1964), who attributed some of the differences in the digestibility and conversion of host plants of Manduca sexta (Johan) to differences in their moisture content.

Plants vary in their content of nutrients as well as secondary plant compounds. These variations are dependent not only on the taxonomic differences but also on the plant part, developmental stage, physiological condition of the plant, to name a few. These factors have been shown to influence both the behaviour and the development of plant feeding insects.

Among the plant species included in the present study, different species have shown various degrees of suitability to A. pisum. Generally, field peas and alfalfa appear to be the most acceptable hosts to A. pisum. However, there are different levels of suitability among various varieties/cultivars within any given species. For instance, different pea varieties, Perfection, Pride and Onward, have been shown to host A. pisum in three significantly different ways (Harrington 1945; Cartier 1959; Maltais and Auclair 1962). Poor survival and development of A. pisum on some hosts may be due to a nutritional deficiency (Maltais and Auclair 1962) or may be due to lower ingestion or some secondary plant chemicals

which inhibit or deter feeding. The factors leading to differences in the resistance of plants to insects are inadequately known. The clones of pea aphid behave in very different ways to the same variety of plant species and thus to the same food. Although it is beyond the scope of the present study, it would be very important to study why the clones diverge so greatly in their reactions to the same variety of plant. Investigations of this nature will go a long way in solving the problem of the resistance of plants to aphids.

2. Life History and Biology of A. pisum

The life cycle of aphids is a complex sequence of events involving a series of different forms, the transition from one form to another being triggered by changes in the environment (Lees 1966; Hille Ris Lambers 1966). A feature of this life cycle which is found in most species of aphids is cyclical parthenogenesis, in which a series of thelytokous parthenogenetic generations in spring and summer are combined with a single annual sexual generation. Usually sexual morphs are produced in late summer or autumn and the aphids overwinter as eggs. This is a complete cycle or holocycle. Life cycles involving continuous all-year-round parthenogenesis (anholocycly) are derived secondarily from the holocycle (Blackman 1974). Lees (1966) considered that the anholocyclic character most probably arises as a gene mutation, and Muller (1971) has come to the same conclusion after rearing holocyclic aphids of seven species for up to 15 years without loss of the ability to produce sexual forms. The pea aphid exhibits either holocycly or anholocycly, or a combination of both, according to the environmental conditions

they encounter in different regions (Cooke 1963).

Perhaps of more fundamental significance are the genetic implications of this life cycle variation, because holocycly and anholocycly are likely to have different effects on the genotypic composition of aphid populations. The sexual phase of the aphid holocycle entails genetic recombination between genotypes. Populations of aphids which have overwintered parthenogenetically may consist of lesser numbers of old clones than the populations of aphids which have overwintered as eggs, physiologically and perhaps genetically adapted to winter survival on one host plant. In Manitoba, A. pisum is holocyclic and overwinters as eggs deposited on perennial legumes (Fig. 1).

The biology of A. pisum has been studied principally in Europe and North America over recent decades. The number of generations of pea aphids varies in different parts of the world. Folsom (1909) reported 17 generations in the first-born line in the state of Illinois. According to a study by Davis (1915) in Indiana, between March 31 and December 31, there were 19 generations in the first-born line, and on average of 13 generations. Smith (1916) reported 21 generations in Virginia, Campbell (1926) 14-28 generations in California, and Harrington (1941) 15-16 generations in the state of Wisconsin in one season. Markkula (1963) reported that in Finland, the maximum number of generations produced in one season was 9-10 in the first-born line, thus the average number of generations produced was 6-7. There are no reports of the number of generations of the pea aphid in Manitoba. Because of the lower temperatures and shorter growing seasons in Manitoba,

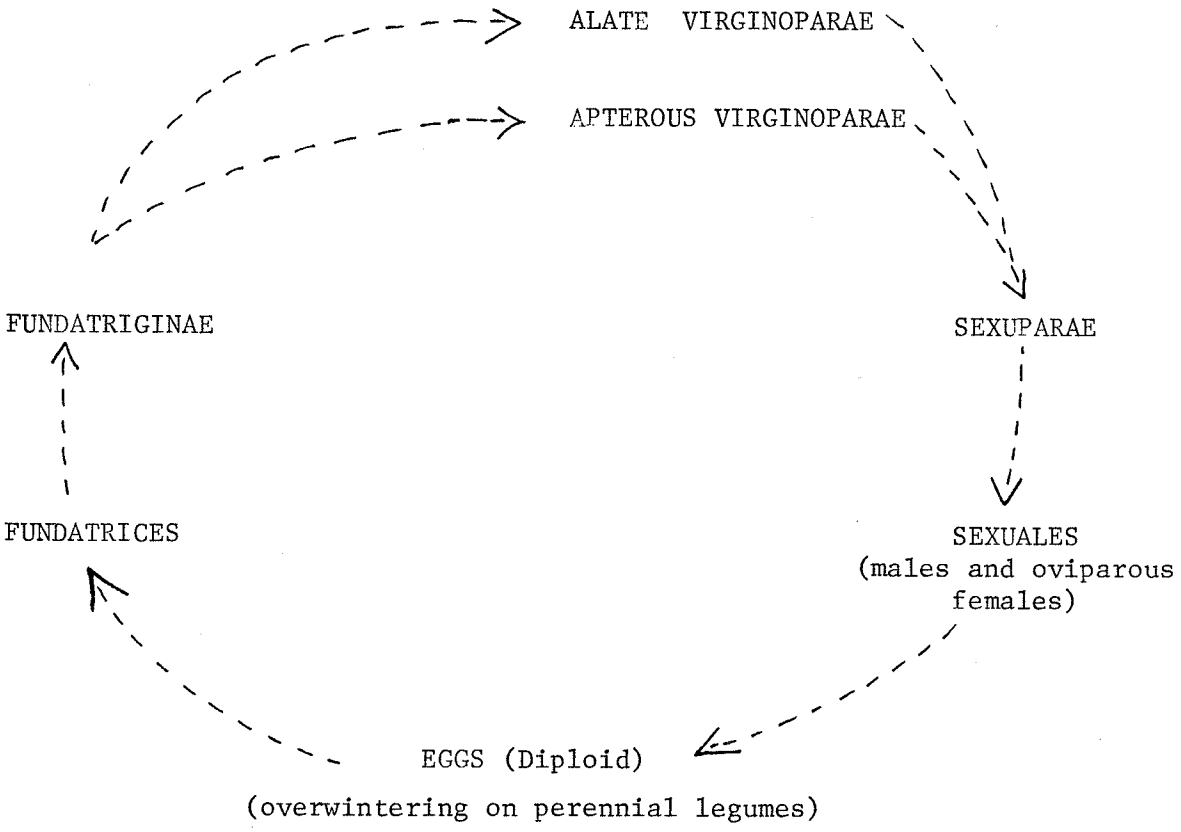

Figure 1. Life cycle of the pea aphid, Acyrthosiphon pisum (Harris) in Manitoba.

the number of generations produced would be expected to be lower than in the USA, and it may be that the situation is quite comparable with that of Finland.

Little is known of the comparative biology of holo- and anholocyclic aphids. Tamaki et al. (1982a) reported that an anholocyclic strain of M. persicae, which overwintered in the viviparous stage, exhibited some degree of cold tolerance compared to the holocyclic strain tested.

There are numerous reports in the literature on the length of the various phases of the life cycle of A. pisum. Temperature data, however, are sometimes lacking. The pre-reproductive period has generally been reported to be 9-12 days (Smith and Davis 1926; Cartier 1960; Markkula 1963; Sylvester and Richardson 1966; Murdie 1969; Frazer 1972; Siddique et al. 1973; MacKay and Wellington 1975). According to the above mentioned workers, the average length of reproductive period was approximately 15-20 days. However, Markkula (1963) reported it to be 25-31 on red clover. The average length of the post-reproductive period was reported to be 10 days by Cartier (1960), 4-6 days by MacKay and Wellington (1975) and 15-21 days by Markkula (1963). The average length of life is generally around 30 days (Cartier 1960; MacKay and Wellington 1975), at temperatures around 20^{o}C. It appears, however, that the average length of various phases of the life cycle depends, to a great extent, on the host plant, temperature, and other environmental factors.

The pea aphid appears to be fairly prolific and a great number of investigators have determined the number of progeny produced by agamic

females. Average figures reported for number of progeny generally range between 60-95. Campbell (1926) reported 68 (apterae, 71.7 and alatae, 58.3), Harrington (1943) 68-72, Kenten (1955) 77-86, Siddique et al. (1973) 83.7, MacKay and Wellington (1975) reported for 95 for apterae and 86 for alatae and Murdie (1969) 117. The largest numbers of offspring noted per female are 176 (Campbell 1926) and 175 (Knowlton and Sorenson 1937). Mean daily fecundity ranged between 8 (Siddique et al. 1973) and 12 (Murdie 1969).

The species and variety of host plant have a considerable effect on the number of progeny produced by the pea aphid. Reproduction is very great on certain susceptible pea varieties such as Perfection and considerably less so on resistant varieties (e.g. Pride and Onward) (Harrington 1941; Cartier 1959). This fact, as well as the differences in reproductive capacity of various biological races (Frazer 1972) explain to some extent, the rather wide divergences in numbers of progeny found by the above investigators.

Markkula (1963) studied the numbers of progeny produced by fundatrices of A. pisum and he found that the reproductive capacity of the fundatrices was clearly greater (20-40%) than that of the following generations of agamic females. Markkula (1963) also claims that this feature seems to be characteristic of several aphid species including Brevicoryne brassicae (L.).

Very few investigations have been performed on the biology of sexuals of A. pisum. This is understandable, since in tropical areas this species does not produce any sexuals and reproduction is usually partheno-

genetic. The sexual females of the pea aphid are apterous. Among the males, however, both alate and apterous forms are known. The general view is that in North America alate males are more prevalent while in Europe, by contrast, the males are usually apterous. Markkula (1963) reported that there was no difference in length of life of sexual females when reared on red clover and on peas in Finland. He reported the average values to be pre-reproductive period 27 days, reproductive period 35.3 days, post-reproductive period 16.3 days and total life span 78.6 days. Markkula (1963) reported that average number of eggs laid was 23. He also claimed that this was one of the highest figures known for aphids.

3. Effects of Host Plants on Aphids

It appears that plants vary in the degree to which they support the survival, growth, and development of aphids. Likewise the responses of aphids to host species under test may vary not only with differences between aphid strains but also with previous experience. For instance, Myzus persicae, settles more readily on sugar-beet if taken from cultures on Chinese cabbage than from cultures on other hosts (Russell 1966). Lowe (1973) also found some evidence on M. persicae to support the observations made by Russell (1966). Similar preconditioning effects occur in other aphids (Schizaphis graminum (Rondani), Macrosiphum avenae (Fb.) and Rhopalosiphon maidis (Fitch))infesting cereals (Apablaza and Robinson 1967). Wilson and Starks (1981), however, observed very little preconditioning effects in the greenbug, S. graminum, reared on five different plant species.

Auclair (1966) took seven strains of A. pisum from alfalfa and reared them on peas for seven months, but did not observe any kind of conditioning. Markkula and Roukka (1970b) found distinct conditioning of A. pisum to red clover over one year in only one clone out of three tested. Therefore, it appears that the phenomenon of conditioning of A. pisum is a clonal characteristic rather than a species characteristic.

The host plant can also affect the behaviour and physiology of aphids in other ways. For instance, it can be responsible for the determination and development of alates (Markkula 1963; Sutherland 1967, 1969; Woodford 1969). Markkula (1963), in studying two strains of A. pisum, found that both produced more alatae on pea than on red clover, and concluded that the kind of host plant had an effect on the production of alates. Cartier and Painter (1956), in their study of the corn leaf aphid, R. maidis, noted that the ratio of apterous and alate aphids varied with the hosts and biotypes. They also found that biotypes of this species could be differentiated on the basis of the number of alate and apterous adults produced by the original apterous females when reared on different varieties of host plant. Sutherland (1969) observed more alatae in the progeny of crowded females of A. pisum caged on mature bean leaves than uncrowded females. He also reported that fewer alatae were produced by females caged on excised mature pea leaves fed with glucose and amino acids than on leaves fed with a pure glucose solution. Aphids, Sitobion avenae (F.) and Rhopalosiphum padi (L.) feeding on oats infected with barley yellow dwarf virus produce more alatae than on uninfected oats and this might favour the spread of virus (Gildow 1980).

There were no reports on the effects of different host plants on A. pisum populations as a whole in the field. It is likely that when the season progresses from early to late, a pea aphid population on a particular host may show some adaptation to the same host. When such populations are tested at different times of the season, if there is such an adaptation, that could be measured by their differential survival, fecundity, alate production etc. on different hosts.

4. Variation and Insect Biotypes

When considering any type of intraspecific variation, a major problem is determination of the extent to which it is due to genetic differences within the species, and the extent to which it is influenced directly by the environment. In aphids, every fundatrix will differ genetically from every other fundatrix as each has arisen from a different fertilized egg. Each is therefore founder of a distinct clone.

Anholocycly of aphids in the tropics could be due directly to lack of the environmental stimulus needed for production of sexual morphs. In temperate climates, the occurrence of both holocycly and anholocycly in the same regions under identical climatic conditions makes it clear that genetic differences are involved, and experimental work indicates that these differences are a feature of the variation within as well as between local populations (Blackman 1971).

Intrapopulation variation is exhibited in a number of ways. Wool and van Emden (1981) suggested that different abilities of M. persicae clones to adapt to an artificial diet is genetically based. They found only five clones survived the 10th generation on artificial diet out of

the 64 clones tested. Masaki (1961) gave several examples of species with differences in diapause duration.

The precise biological nature of this variation, however, is still poorly understood. Conflicting suggestions, based on little experimental evidence, have been made concerning the degree of genetic differentiation. Some workers have reported such variations, among clones of A. pisum having diverse geographic origins and have termed them biotypes (e.g. Cartier et al. 1965; Auclair 1978). The scope of the pea aphid biotypic differences with regard to their geographic distribution will be discussed below.

The existence of genetic variability in the capacity to overcome crop varietal resistance is a well recognized phenomenon among insect species. Such genetic and physiological strains of insects are commonly referred to as biotypes. Many species of aphids have been found to consist of a complex of biotypes (Eastop 1973). A complicated genetic interaction has been demonstrated between the Hessian fly, Mayetiola destructor (Say) and wheat varieties (Gallun 1977; Sosa 1978, 1981), and in the genus of flies Rhagoletis (Bush 1969). The case of the brown plant-hopper, Nilaparvata lugens Stal, and the rice varieties has been the subject of study by many workers (Sogawa 1980, 1981; Pathak and Heinriches 1982 and references therein).

Biotypes are usually recognised by a biological function rather than by morphological characters. These biotypes have been recognised by a variety of characters, including differences in life cycles, host plant preferences, susceptibility to insecticides, virus transmitting

abilities, feeding behaviour, reaction to light and susceptibility to pathogens. Numerous authors have used the words "races", "strains", and "lines" instead of biotypes. In this review, these words will be used interchangeably, as used by the authors concerned.

Muller (1966) regards the anholocyclic tropical populations of Lipaphis erysimi (Kitb.) and Aphis craccivora Koch as races of their respective European holocyclic species. Muller (1969) has described a population of Aphis nasturtii (Kltb.) which prefers Calla to potato as a secondary host plant but both populations alternate on Rhamnus.

Cognetti (1965) recognised different strains of Brevicoryne brassicae (L.) by their biologies and Lammerink (1968) recorded a strain of B. brassicae which colonised previously resistant varieties of crops. Giliomee et al. (1968) found populations of the wooly apple aphid, Eriosoma lanigerum (Hausmo) which can colonize previously resistant varieties of apples. Blackman (1971) gave accounts of the biologies of clones of M. persicae derived from specimens collected on different crops and at different localities, with special reference to the proportions of different biotypes found on different crops. Tamaki et al. (1982b) reported that a holocyclic strain of M. persicae was more successful in transmitting beet western yellow virus (BWYV) to shepherds-purse, Capsellabursa pastoris (L.), than the anholocyclic strain.

Rochow and Eastop (1966) described a population of Rhopalosiphon padi (L.) in which hot weather dwarfs had both an unusual wing venation and an increased virus transmitting ability. Rochow (1960) reported that strains of the greenbug, Schizaphis graminum (Rondani), differ in their ability

to transmit the Barley yellow-dwarf virus (BYDV). Orlob and Arny (1960) studied the transmission of BYDV by different biological forms of the apple grain aphid, Rhopalosiphum fitchii (Sanderson), and concluded that vector specificity rests with characters which are genetically fixed. Saksena et al. (1964) reported that various biotypes of R. maidis differed in transmission efficiency of BYDV. Jones (1967) found two races of A. craccivora with different abilities of transmitting groundnut rosette virus.

In corn leaf aphid, R. maidis, the occurrence of two races was reported by Cartier and Painter (1956). Pathak and Painter (1959) provided evidence for the occurrence of two more biotypes and went on assigning various populations all over Kansas to the said four biotypes (KS-1 to KS-4), on the basis of their fecundity. Similarly, six biotypes of the spotted alfalfa aphid, Therioaphis maculata (Buckton), have been recognized in the Western United States (Nielson et al. 1970).

The first observations on the resistance of pea plants to the pea aphid, A. pisum, were published as early as the 1920's (Russell and Morrison 1924). Searls (1932) recorded the occurrence of resistance in some varieties of peas to A. pisum. Harrington (1941) first demonstrated the existence of biotypes in A. pisum. Harrington (1945) kept 31 pure parthenogenetic lines collected from different parts of the USA and concluded that there were at least five biotypes in the United States, separable on the basis of body size, feeding injury, and rates of reproduction on peas (varieties - Perfection, Pride and Onward). He observed, on the var. Perfection, among the 31 lines tested for their

fecundity, a line A41 collected from Alabama which had the highest fecundity figure (97.4 progeny/female) as against the lowest figure (48.3 progeny/female) exhibited by a clone collected from Virginia. Likewise on the var. Pride, a clone from Hamilton, Mont., had the largest fecundity (89.7) and the smallest fecundity figure was 25.1 progeny/female of a clone from Virginia (V-42). On the var. Onward, a clone from Alabama had the largest fecundity figure (88.0) while the Virginia clone V-42 had the smallest (16.0).

Cartier (1957, 1959 and 1963) investigated 23 separate clones and recognized three biotypes in Quebec on the basis of weight and rate of reproduction on three varieties of pea. Two of these biotypes (R_1 and R_2) originated from St. Jean and the third (R_3) was from Waterloo, Ontario. On the var. Perfection, fecundity figures (mean progeny/3 females) were 190, 130 and 100 for the biotypes R_1, R_2 and R_3 respectively. On the var. Pride the figures were 170, 80 and 80 while on the var. Onward, the figures were 70, 20 and 40 for the biotypes R_1, R_2 and R_3 respectively.

Cartier *et al*. (1965) tested two biotypes, one from Quebec (C61-86) and the other from Kansas, on different varieties of alfalfa. On the var. Buffalo, the Quebec biotype had a mean of 21.75 progeny/3 females while the Kansas biotype had 40.75 progeny/3 females at 70^{o}F. Likewise on the var. Ladak 84.25 and 43.0, on the var. Du puits 7.50 and 46.75, and on the var. Atlantic 66.75 and 39.75 for the Quebec biotype and the Kansas biotype respectively. Frazer (1972) recognized five biotypes in British Columbia, collecting one each from the hosts

bean, broom, clover and the remaining two from alfalfa at two different locations. Their range of net reproductive rate on broad bean varied from 91.0 for the bean biotype to 53.3 for the broom biotype. Auclair (1978) had six clones from diverse geographic areas tested on broad bean, peas and artificial diets. Two of them came from Quebec, one each from New Mexico and Kansas in the USA, and the remaining two from France. On broad bean, the green biotype from France had 11.5 progeny/female/day and the Kansas biotype had 9.0 progeny/female/day which were the largest and the smallest figures. Likewise on peas, the green biotype from France had 9.9 and the Ileaux Condres (Quebec) biotype had 4.7 progeny/female/day, the largest and the smallest figures. Adult weights varied from 4.8 mg. for the Kansas biotype to 4.1 for the St. Jean (Quebec) biotype on broad bean. On peas, the green biotype from France had the heaviest weight 3.9 mg. as against the lightest figure 1.8 mg. for the Ilenux Conderes (Quebec) biotype.

Muller (1962) separated nine strains collected in the field by observing the maintenance of populations on eight species of Papillionaceae. He distinguished the strains on the basis of preferred host plants. Markkula (1963) observed that the green forms of A. pisum were more fecund than the red forms and that, although both forms produced more alatae on pea than on red clover, the proportion of alatae among progeny did not differ in the two forms irrespective of host. Lowe and Taylor (1964) found green and red lines of A. pisum that also differ in alary polymorphism and behaviour patterns and described quantitative evidence of these differences. Neiman (1971) tested 31 field collected

lines of A. pisum and assigned them to eight biotypes based on significant differences as measured by mean adult dry weight, reproduction and survival on four leguminous hosts. Milner (1982) reported two biotypes of A. pisum occurring in Australia separable in their susceptibility to an isolate of the fungal pathogen, Erynia neoaphidis Remaudiere and Hannebert. A dosage which killed an average of 94% of one biotype did not kill a single aphid in the other.

Muller (1971) reported that in hybridization experiments, it was possible to obtain hybrids of several biotypes of A. pisum. He further reported that it was possible to obtain a viable hybrid between a pea-attacking form and one form which colonizes Trifolium pratense L. as its principle host plant and cannot colonize on the pea.

Meier (1964) investigated how far morphological differences of A. pisum could be considered an indication of biological separation, but was unable to discern any differences among the biotypes attacking different host plants. Thottappilly et al. (1977) examined morphological differences between two biotypes of A. pisum. They observed differences in pigmentation as well as other morphological differences between the two.

According to Eastop (1973)*, a biotype

> "is a taxonomic concept mostly used by non-taxonomists, and it has been defined as consisting of all individuals of equal genotype. In aphids at least, and probably elsewhere, equal genotype means behaving similarly as far as researcher's immediate interests are concerned".

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*Eastop, V.F. (1973), Biotypes of aphids, p. 40, In 'Perspectives in aphid biology' Ed. by A.D. Lowe, Bull. No. 2, Ent. Soc. New Zealand, DSIR, Auckland, 123 pp.

Maxwell and Jennings (1980)* define the term biotype as

> "an individual or population that is distinguished from the rest of its species by criteria other than morphology, for example, a difference in parasite ability".

Biotypes of A. pisum have been studied in Australia (Milner 1982), Canada (Auclair 1978; Cartier 1957, 1959; Cartier et al. 1965; Frazer 1972), Finland (Markkula and Roukka 1970a, 1970b, 1971), France (Bournoville 1977a, 1977b), Germany (Muller 1962, 1971, 1980), Italy (Frohlich 1962), Switzerland (Meier 1976), and in the USA (Harrington 1941, 1945) over the past decades. However, it appears that in most of the studies, although 'the biotypic phenomenon' has been clearly documented, the exact biological nature of such biotypes and their precise relationship with host plants and/or geographic location has not been adequately documented.

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*Maxwell, F.G. and Jennings, P.R. (Eds.) (1980). Breeding plants resistant to insects, p. 618, John Wiley, New York, 683 pp.

CHAPTER III

MATERIALS AND METHODS

This study was conducted in the field as well as in the laboratory and the methods for the two areas of work differed somewhat. Hosts included in the field studies were: alfalfa (Medicago sativa L. var. Beaver), sainfoin (Onobrychis viciaefolia Scop. var. Melrose), birdsfoot trefoil (Lotus corniculatus L. var. Leo), sweetclover (Melitotus officinalis L. var. Yukon Yellow blossom), field peas (Pisum sativum L. var. Trapper) and fababeans (Vicia faba minor L. cv. Diana). In the laboratory alfalfa (varieties Beaver and Algonquin), sainfoin (var. Melrose), trefoil (var. Leo Birdsfoot), and fababeans (cv. Diana) were used.

Experiments were designed so as to document the responses of aphids to different host plants, sampled from various populations. Field transfers of aphids were made among plots of different hosts with the primary objective of estimating mean survival to reproduction and mean fecundity. However, in the field experiments, replication within any clone was not possible, although this was done in the laboratory experiments. Laboratory experiments were of two types. Survival experiments were primarily intended to estimate mean nymphal survival and adult dry weights while fecundity experiments were conducted to estimate mean fecundity and alata production.

1. Laboratory Studies

i. Aphid cultures

Aphids were collected using sweep nets. To assure that the aphids and their resultant clones were representatives of the population in each field, sweep samples were taken from different parts of the field, excluding a 2 m band around the edge where recent immigrants were most likely to be present (Lewis 1969).

Cultures of a single clone were started from one wingless virginoparous female which was placed on excised leaves of fababeans on moistened paper towel in 60 x 15 mm size petri dish (Fig. 2). Undamaged leaves of fababeans were selected from plants in the eight-leaf stage. Neither the top nor the bottom pair of leaves were used. Plants were grown in a perlite-vermiculite mixture and watered with a nutrient solution (Appendix 2). All aphid cultures were maintained in a growth-chamber where temperatures were set at $20^{\circ}C \pm 1^{\circ}C$ and the photoperiod was 17L:7D. The relative humidity ranged between 50-70%.

ii. Plant cultures

The plants to be tested were grown in a non-sterilized soil mixture (1 soil: 1 sand: 1 peat) in plastic pots 12.5 cm in diameter and 10 cm in height. Pots were seeded with an unknown number of certified seeds in each case, and after germination the plants were thinned to one per pot. Plants were first used for tests about 1½-2 months after seeding. For subsequent experiments, the top growth was removed by cutting at ground level, and the plants were allowed about ten days for re-growth

Figure 2. Aphid cultures in petri-dishes.

before use in experiments. Plants were watered as necessary.

iii. Growth-chamber conditions

All laboratory experiments were conducted in a walk-in plant growth chamber in which temperature was maintained $20^{o}C \pm 1^{o}C$ and photoperiod set at 17L:7D with light intensity of approximately 2300 lux at cage level. The relative humidity ranged between 50-70%.

iv. Experimental procedures

(a) Fecundity experiments

Fourth instar apterous aphids were caged individually on hosts using clip-on cages (Fig. 3). Early-born progeny (first 5-7) of a mother were used. The cages were examined at least every other day and counts of progeny of each aphid were made. At each inspection, the new nymphs were removed using a camel-hair brush and without disturbing the mother. Nymphs were reared on excised fababean leaves in petri dishes in order to determine their morph.

At least ten replicates for each clone-host combination were carried out unless otherwise stated. Excised fababean leaves in petri dishes were included as a treatment in all the experiments.

(b) Survival experiments

First instar nymphs born within the previous 12 hrs were placed on hosts and the plants were caged using whole plant cages (Fig. 4). Mortality was recorded at least every other day and the time taken to become adult (nymphal development period) was recorded. As soon as they

Figure 3. Clip-on cages.

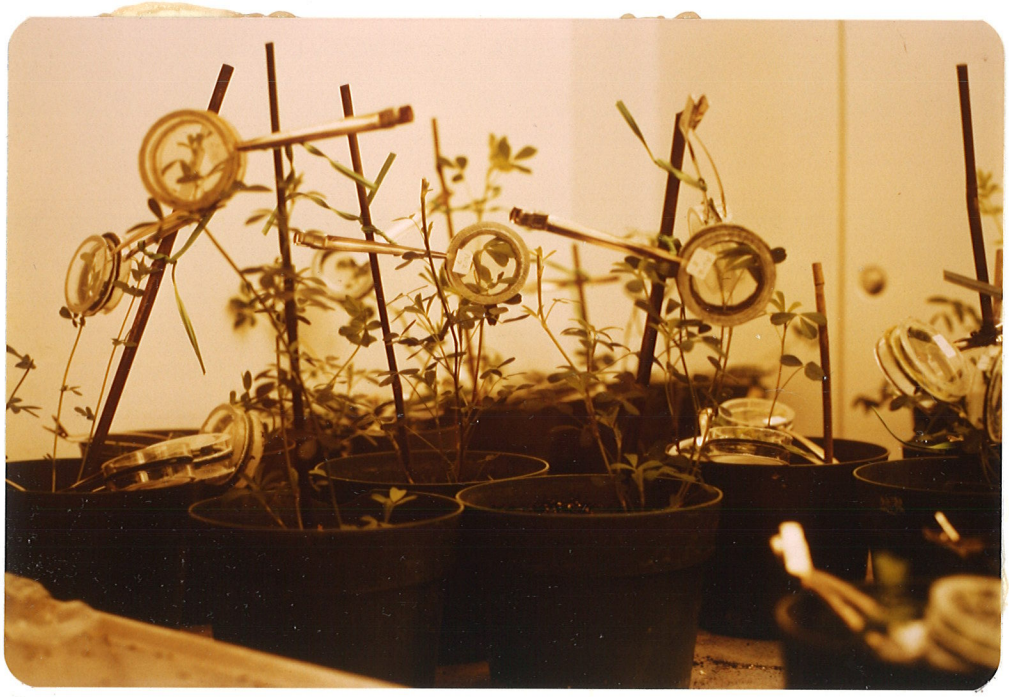
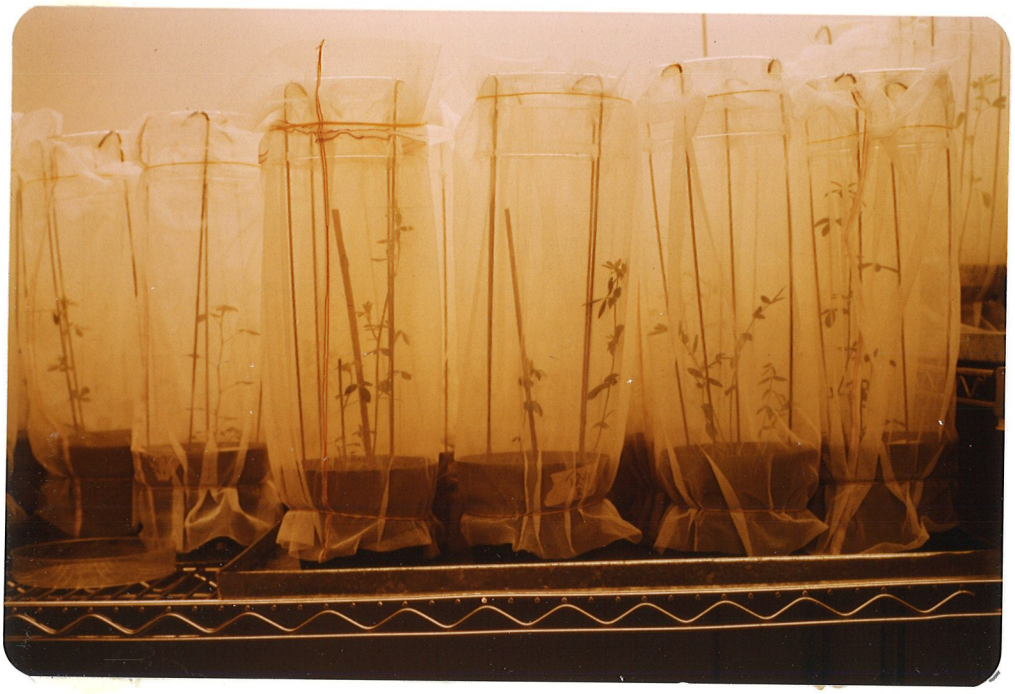


Figure 4. Whole plant cages.



became adults, before they began reproduction, aphids were placed singly in 12 x 75 mm culture tubes and dried at 80°C. After 48 hours dry weights were taken using an automatic electrobalance (Cahn Model 25).

v. Clones tested

(a) 1980

Three aphid clones were collected, one each from fields of alfalfa, trefoil, and sainfoin at the Research Station, Glenlea, Manitoba, during mid-season (20 July 1980). These fields had been seeded to their respective crops in early May, 1980. These three clones were tested in the laboratory throughout 1980/81, and experiments were repeated several months apart. The three clones were coded as AL-80 (collected from alfalfa), TR-80 (collected from trefoil), and SA-80 (collected from sainfoin).

These three clones, particularly AL-80, were used as standard checks in experiments conducted in 1981 and 1982.

(b) 1981

During the crop season of 1981, sixty clones collected from the same fields of alfalfa, trefoil and sainfoin at the Research Station, Glenlea, Manitoba, were tested in the laboratory. Two collections were made: the first consisting of thirty clones, ten each from alfalfa, trefoil and sainfoin, collected early in the season (09 June 1981), while the second consisted of thirty clones, ten from each host, collected later in the season (29 July 1981).

In fecundity experiments, the fecundity of each female during the

first seven days of reproduction was measured as facilities prevented life-long counts such as was done in the case of 1980 clones. Similarly, only the first 20 progeny of each female were reared to monitor the morph. In 1980 and 1981 experiments, only one variety of alfalfa (var. Beaver) was used.

(c) 1982

In 1982, it was decided to test the populations existing on older stands of hosts and also to test two varieties within a host. Accordingly, a six year old alfalfa field (var. Algonquin) at Dugald, Manitoba, and a four year old alfalfa field (var. Beaver) at the Research Station, Glenlea, were selected. The distance between these fields was approximately 50 km.

Twelve clones were collected on 30 May 1982, from Dugald, and 12 clones from Glenlea on 28 May 1982. The second collection was made later in the season: 12 clones from Dugald on 16 July 1982, and 12 clones from Glenlea on 30 July 1982. These clones were tested in the laboratory using procedures similar to those of 1981, except that survival experiments were not carried out in this case.

2. Field Studies

i. 1980 and 1981

Field transfers were made during the crop seasons of 1980 and 1981, among the plots of alfalfa, sainfoin, trefoil, sweet clover, field peas, and fababeans, especially grown for the purpose at the Research Station, Glenlea. Fields were seeded to the crops in early May 1980, and the

recommended agronomic practices laid down by the Manitoba Department of Agriculture were followed (Anonymous 1980).

Fourth instar apterous nymphs were caged singly using sleeve cages (Fig. 5), and the branch of the plant along with the cage was removed after 160 day-degrees above base 4°C and brought in the laboratory for examination. Parameters estimated were mean survival to reproduction, mean fecundity, and mean proportion of alatae in the progeny. This work was carried out throughout the growing season at variable intervals to examine whether there was any change over the season in extent of variation in the effects of host plant on the aphid populations.

ii. 1982

Because of the easier and more precise handling possible inside the laboratory, it was decided to test the field-collected aphids in the laboratory. Thus field-collected fourth instars were placed directly on different host plants in clip-on cages and placed in the growth chamber where other laboratory experiments were conducted. After about 160 day-degrees above base 4°C, their survival to reproduction and total fecundity were recorded.

Analysis of variance and tests of significance were carried out as outlined by Steel and Torrie (1980). Chi-square tests and orthogonal comparisons were done as outlined by Snedecor and Cochran (1980).

Figure 5. Sleeve cages.

CHAPTER IV

RESULTS

1. Effects of Caging and Rearing Techniques

In order to ensure that different experiments could be compared an investigation was carried out to determine if results would differ if aphids were caged using different types of cages. Fourth instar apterous nymphs were caged individually using different types of cages. Experiments were terminated on the seventh day of reproduction and the total progeny and the number of dead nymphs were counted. Table 1 shows the results. Clip-on cages had drastic effects on the fecundity and nymphal survival. However, it was found that if the progeny produced were removed at least every other day, progeny production in clip-on cages could be raised as high as that in whole plant cages and accordingly nymphal mortality could be minimized. Therefore, in fecundity experiments clip-on cages were used while in nymphal survival experiments, whole-plant cages were used. All the field experiments were done with sleeve cages.

During the study the questions arose as to whether living plants and excised leaves of fababeans differ significantly as hosts of A. pisum. Robinson (1961) found that there was no significant difference in fecundity of A. pisum when caged on upper and lower surfaces of the broad bean leaves. There was no information available on excised leaves versus whole plants as hosts for A. pisum and, therefore, an experiment was conducted. The results obtained are represented in Table 2. There was no significant difference in fecundity per female

Table 1. Effects of different cages on fecundity and nymphal survival on alfalfa. (Clone:-AL-80).

	Whole plant cages	Sleeve cages	Clip-on cages	Clip-on cages (when progeny removed daily)
Progeny/female/* seven days (± S.E.)	52.6 ± 4.6^{A}	46.3 ± 4.5^{A}	22.5 ± 1.8^{B}	48.9 ± 4.8^{A}
% Nymphal mortality* (± S.E.)	1.4^{A}	10.8 ± 2.2^{A}	48.9 ± 3.7^{B}	6.3 ± 1.7^{A}

*Mean of eight replicates.

^{A,B}Means having different superscripts in each row are significantly different at 1% level. (One way analysis of variance and Duncan's multiple range test).

Table 2. Suitability of excised leaves and whole plants of fababeans as hosts. (Clone:-AL-80).

	Whole plants	Excised leaves
Progeny/female/* seven days (± S.E.)	57.1±3.6^{A}	63.4±2.6^{A}
% Alatae* (± S.E.)	0.0^{A}	27.0±2.8^{B}

*Mean of eight replicates.

^{A,B}Means having different superscripts in each row are significantly different at 1% level. (One way analysis of variance and Duncan's multiple range test).

between whole plants and excised leaves ($P>.01$). However, percent alatae in the progeny differed significantly ($P<.01$). In addition, out of the 111 clones tested in the laboratory in 1980, 1981, and 1982, 100 clones produced alatae on excised fababean leaves (Table 3). Questions must now be raised about the suitability of excised fababean leaves and caution ensured in their use as a host in laboratory experiments with A. pisum.

During the present studies, it appeared that for perennials and particularly for alfalfa, even seed certified to be a single variety gives rise to plants of different suitabilities for a given aphid clone. Therefore, it is suggested that in the laboratory experiments, all perennials used may be vegetatively propagated if other resources do not limit this process.

2. Laboratory Studies

i. 1980 clones

(a) Survival

Four hosts (alfalfa, sainfoin, trefoil, and excised leaves of fababeans) were compared for survival and attainment of adulthood for the three clones. First instar nymphs were placed on the hosts and their daily mortality was recorded. As soon as they became adults and before reproduction, their dry weights were taken.

Figures 6, 7 and 8 are graphical representations of percent nymphal survival of AL-80, TR-80, and SA-80 clones respectively. Points at the ninth day also represent the percent attainment of adulthood for all hosts except sainfoin where some nymphal instars were prolonged beyond

Table 3. Production of alatae by 111 clones on different hosts

Hosts	No. of clones producing alatae out of 111 tested	Average % alatae produced by those clones responding (with S.E. and range)
Fababeans (Excised leaves)	100	21.80 ± 3.00 (0.6 - 83.0)
Trefoil (whole plants)	56	10.15 ± 7.27 (0.8 - 66.6)
Alfalfa (var. Beaver) (whole plants)	25	4.75 ± 2.70 (0.9 - 33.3)

Figure 6. Percent survival of clone AL-80 on different hosts (N = 45).

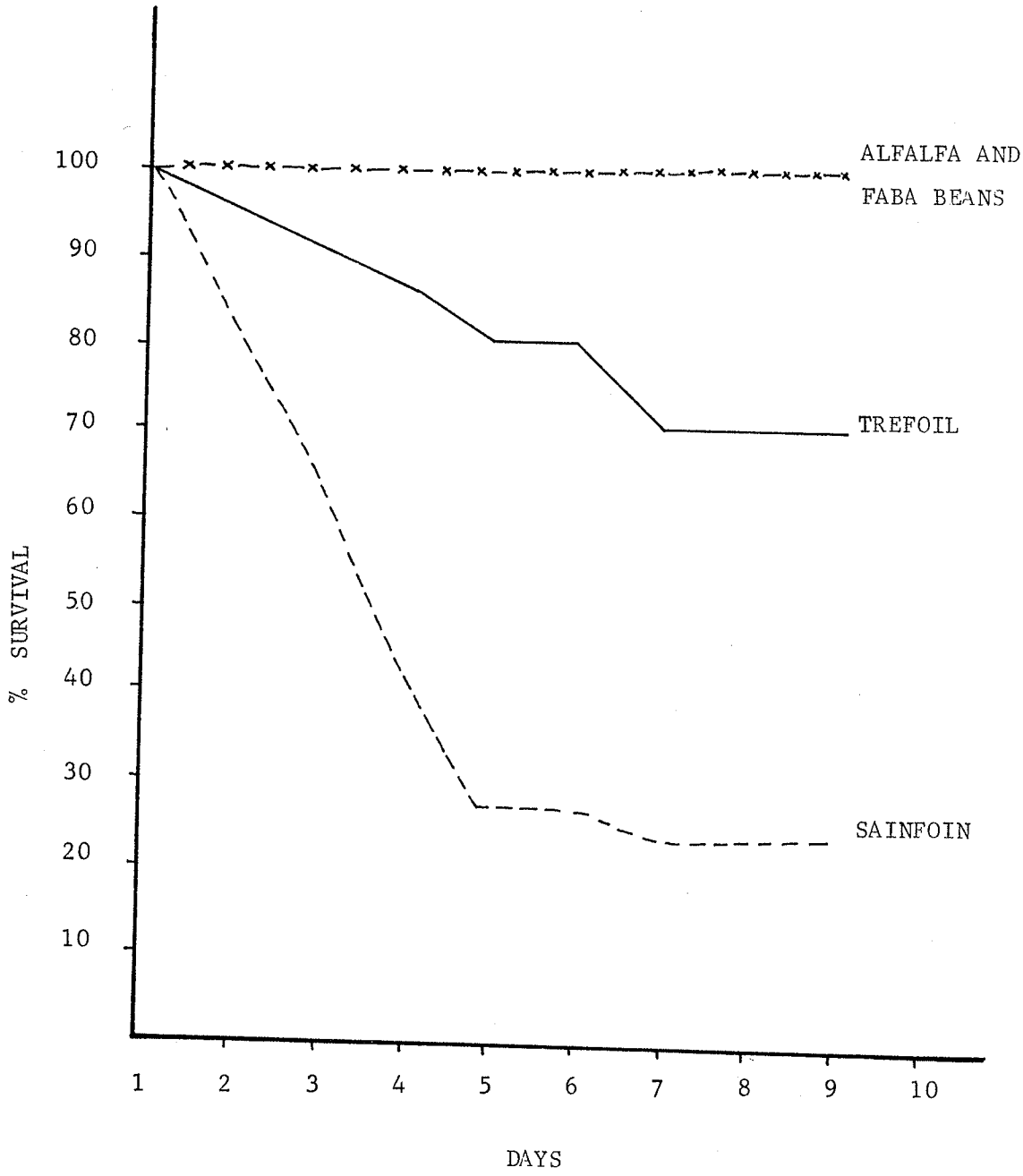

100
90
80
70
60
50
40
30
20
10
% SURVIVAL
1
2
3
4
5
6
7
8
9
10
DAYS
ALFALFA AND
FABA BEANS
TREFOIL
SAINFOIN

Figure 7. Percent survival of clone TR-80 on different hosts (N = 45).

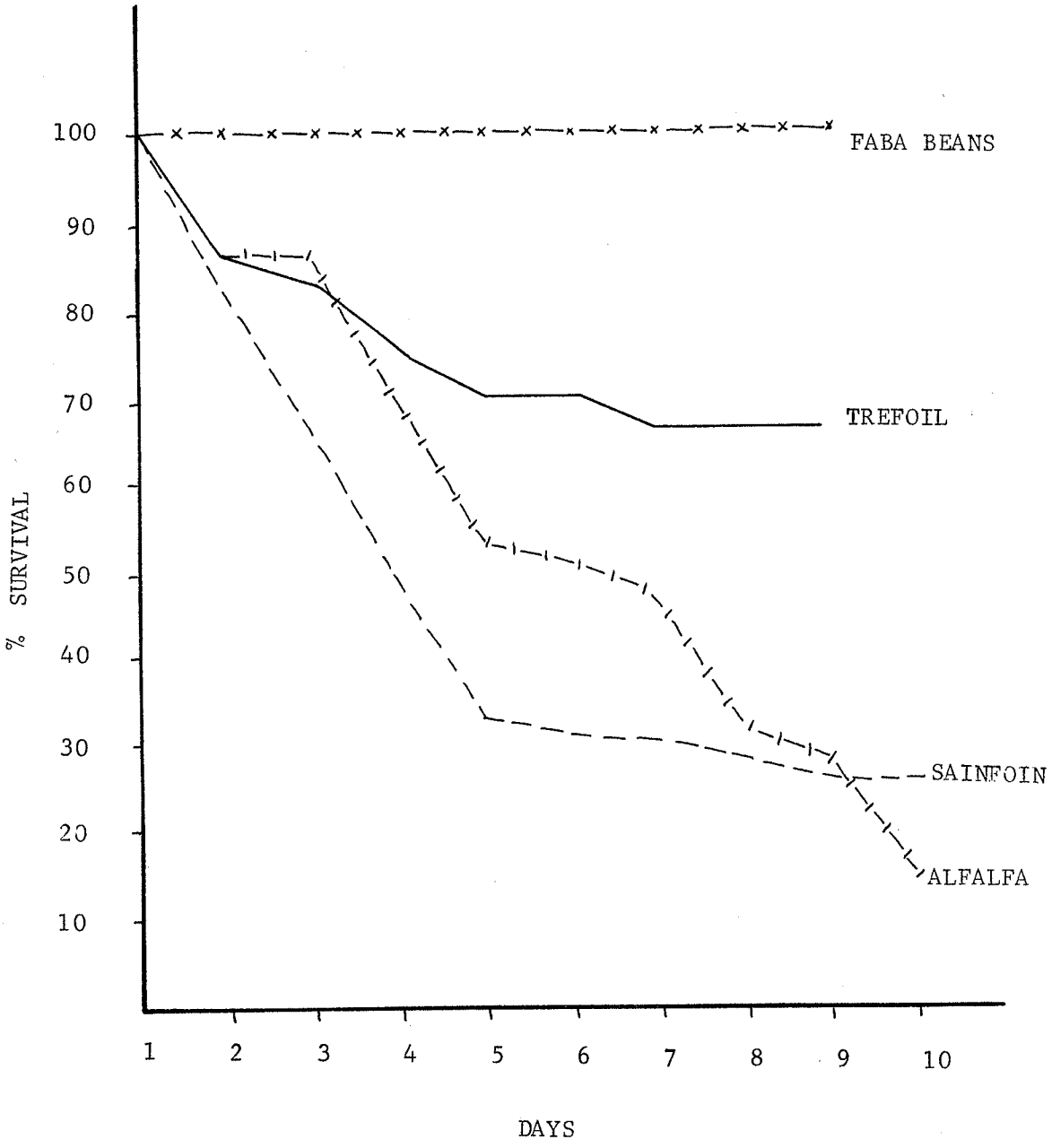
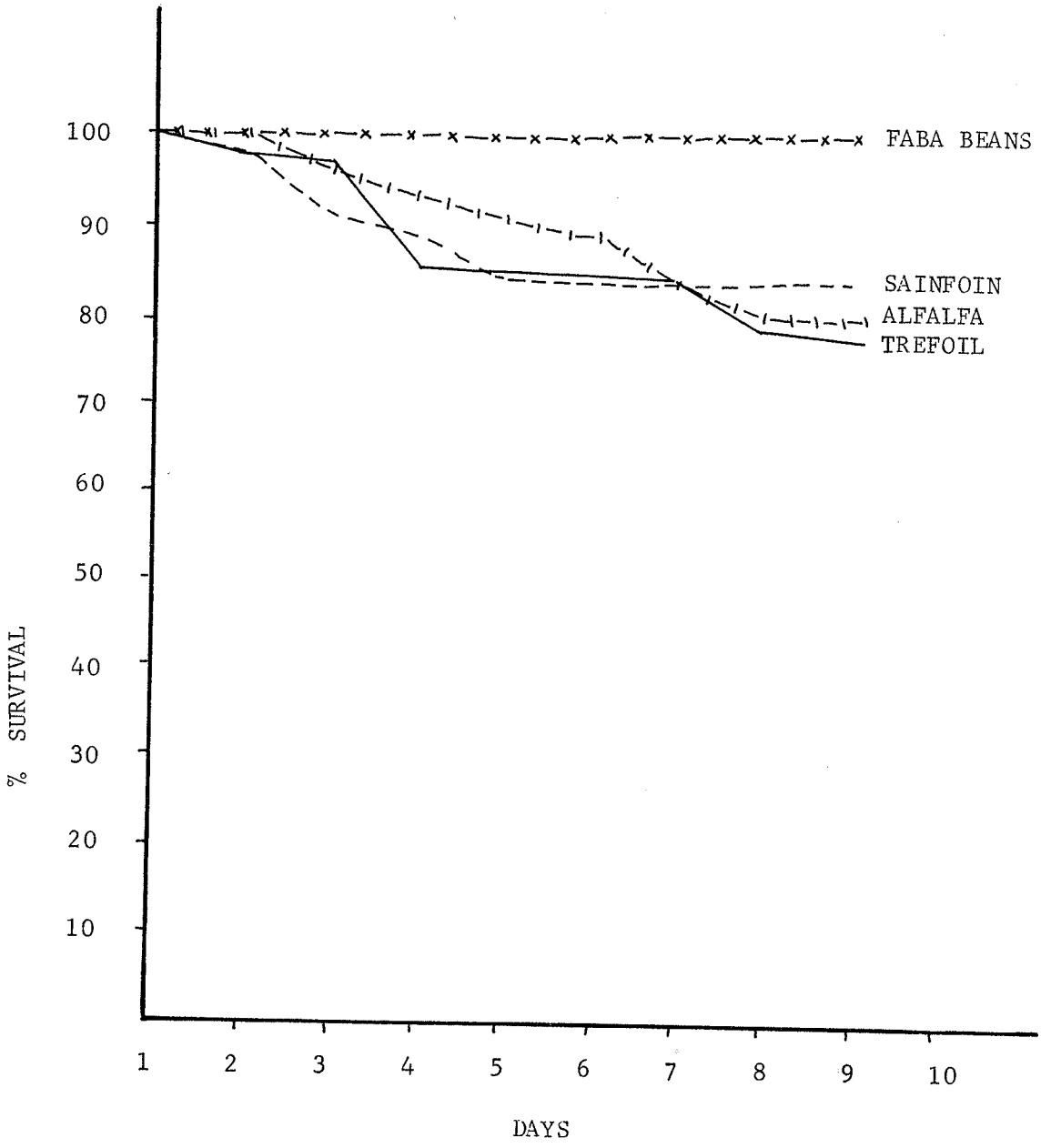

100
90
80
70
60
50
40
30
20
10
% SURVIVAL
FABA BEANS
TREFOIL
SAINFOIN
ALFALFA
1
2
3
4
5
6
7
8
9
10
DAYS

Figure 8. Percent survival of clone SA-80 on different hosts (N = 45).


100
90
80
70
60
50
40
30
20
10
% SURVIVAL
1
2
3
4
5
6
7
8
9
10
DAYS
FABA BEANS
SAINFOIN
ALFALFA
TREFOIL

the tenth day. These figures reveal that all three clones did well on fababeans with 100% attainment of adulthood. On alfalfa, the three clones represent three different patterns (100% for AL-80, 80% for SA-80, and 14% for TR-80). These were significantly different at $P<.05$ according to Chi-square tests done on contingency tables (Snedecor and Cochran 1980). Sainfoin proved to be a poor host for AL-80 and TR-80, although most of the nymphs of SA-80 survived beyond the tenth day but did not become adults.

Figure 9 represents the adult dry weights of the three clones on different hosts. Analysis of variance indicates that on alfalfa the three clones were significantly different whereas on fababeans they were not ($P<.05$). In addition, on sainfoin and trefoil, there was no significant difference.

(b) Fecundity

Fourth instar nymphs were caged singly on the four hosts (alfalfa, sainfoin, trefoil, and excised leaves of fababeans), and their fecundity was recorded daily till the death of the adult. Table 4 shows the data on fecundity, longevity and alate production of the three clones. Both fecundity and longevity of the three clones on alfalfa were significantly different ($P<.05$), while on fababeans longevity was not significantly different. However, clone SA-80 had significantly more progeny ($P<.05$) on fababeans than had AL-80 and TR-80.

(c) Alata Production

The three clones appeared to behave similarly with regard to

Figure 9. Adult dry weights (mg) of the three 1980 clones on different hosts ($\pm$ S.D.).

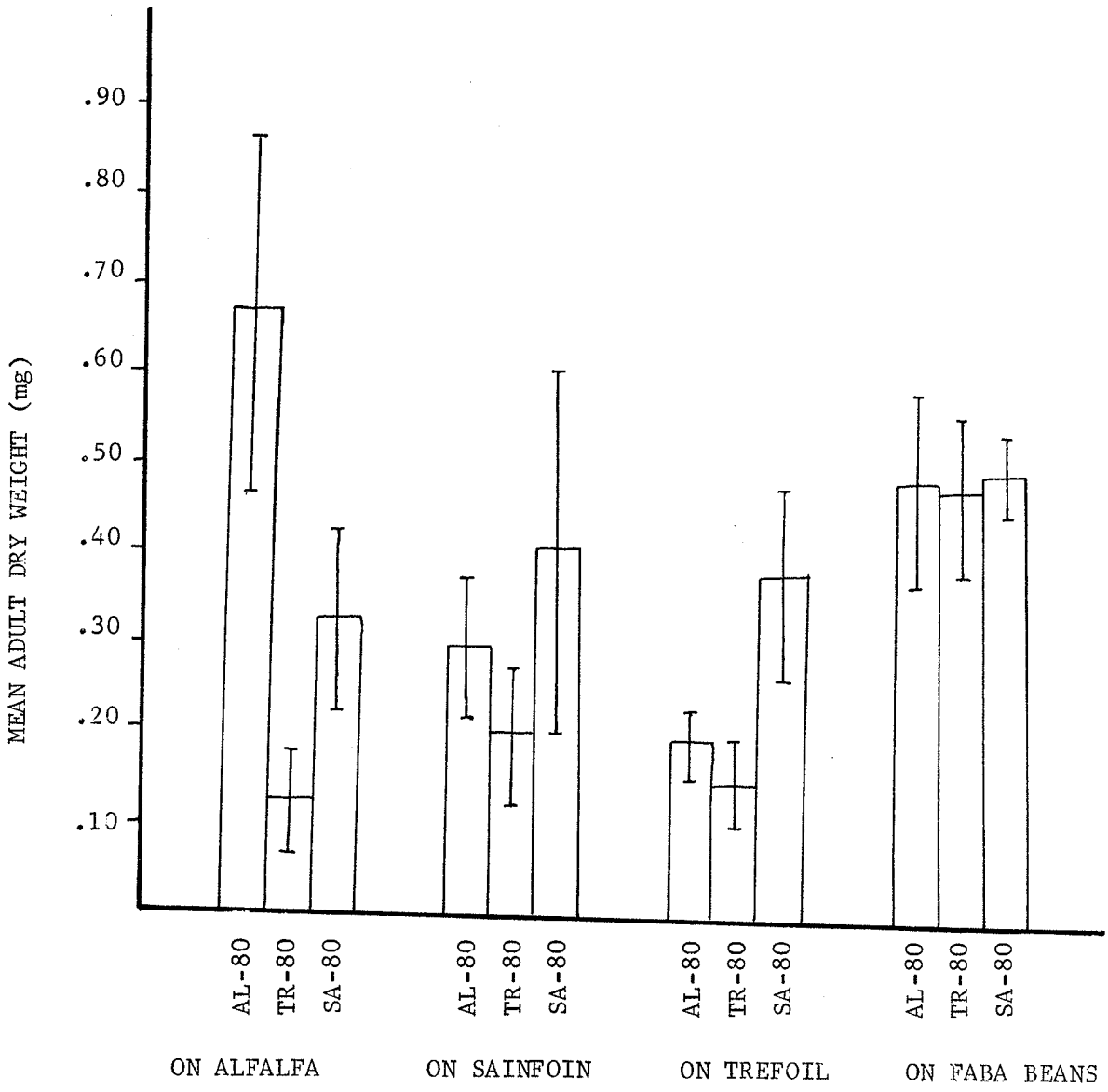

MEAN ADULT DRY WEIGHT (mg)
.90
.80
.70
.60
.50
.40
.30
.20
.10
AL-80
TR-80
SA-80
AL-80
TR-80
SA-80
AL-80
TR-80
SA-80
AL-80
TR-80
SA-80
ON ALFALFA
ON SAINFOIN
ON TREFOIL
ON FABA BEANS

Table 4. Fecundity and longevity of the three 1980 clones reared on different hosts (± S.E.)

Hosts	Alfalfa			Sainfoin			Trefoil			Fababeans		
Clones	AL-80	TR-80	SA-80	AL-80	TR-80	SA-80	AL-80	TR-80	SA-80	AL-80	TR-80	SA-80
Mean progeny/ female	70.2±10.0	0.0± -	34.7±8.6	7.4±2.3	0.5± -	9.9±2.4	1.1± .6	1.9±1.7	5.0±2.6	78.9±7.6	80.0±5.6	108.1±8.0
Mean adult life (days)	22.2±2.2	3.2±2.0	12.2±2.4	6.2±2.8	4.3±2.3	9.1±3.1	3.7±2.3	5.0±2.5	7.0±3.0	23.4±2.4	22.0±2.3	22.7±2.2
Mean alatae (%)	0.0	-	10.0±5.7	0.0	0.0	5.0±4.2	-	0.0	2.0±3.8	28.1±6.3	2.0±4.3	42.1±9.7

Analysis of variance and comparison of means were done on transformed log (x + 1) data. Means within any given host, NOT jointly underlined are significantly different (P<.05) according to Duncan's multiple range test.

one measure, but behaved differently with regard to another measure on the same host. For instance, their dry weights were not significantly different on fababeans (Figure 9) but the clone SA-80 differed significantly from the other two in fecundity on fababeans (Table 4).

When nymphs from fecundity experiments were reared to determine their morph, it was found that the three clones had three significantly different patterns of wing production on alfalfa and on excised leaves of fababeans (Table 4). Therefore, an experiment was conducted to check whether the three clones respond differently or not to a crowding stimulus (Sutherland 1970). Groups of 10 young adults were confined within 5x2.5 mm glass specimen tubes for a period of 24 h. Each aphid was subsequently placed on an excised leaf of fababean in a petri dish. The data (Table 5) reveal that the clones AL-80 and SA-80 are similar but are significantly different ($P<.05$) from TR-80 in response to the crowding stimulus although all three had consistently different patterns of alata production throughout the early experiments (Table 4).

Survival, fecundity, longevity and alata production measurements were repeated three times several months apart during 1980/81, and the three clones responded consistently with regard to parameters estimated on different hosts, showing no significant differences among repetitions ($P>.01$). These clones had been selected for their survival on fababeans at the time of the initiation of aphid cultures. Similarly in case of 1981 and 1982 clones, selection to fababeans occurred at the time of culture initiation. This may be part of the reason why all the clones tested throughout the present laboratory studies generally did well on

Table 5. Alate production by the three 1980 clones following a crowding stimulus on excised fababean leaves

Clone	Percent alatae* (± S.E.)	
	Crowded	Not crowded
AL-80	53.4±11.2[a]	20.9±8.2[a]
TR-80	12.4±4.6[b]	4.0±4.9[b]
SA-80	59.9±8.8[a]	45.2±10.8[c]

*Mean of six replicates.

a,b,c, Means having same superscripts in each column are not significantly different ($P<.05$). (Two way analysis of variance and Duncan's multiple range test).

fababeans.

ii. 1981 Clones

(a) Survival

Clones collected from the field plots of alfalfa, sainfoin and trefoil were tested on alfalfa, sainfoin, trefoil and excised leaves of fababeans. First instar nymphs were placed on the hosts and mortality was recorded every other day. Twenty nymphs were used in each clone-host combination. As soon as they became adults, before reproduction, their dry weights were recorded.

Survival and adult dry weights of different clones from populations sampled during the early season are presented in Table 6 while Table 7 consists of data on clones from populations sampled later in the season. Sainfoin proved to be a very poor host. For most of the clones tested, very few nymphs attained adulthood on sainfoin while in some cases there were none at all. Therefore adult dry weight data on sainfoin has been excluded. The data in Tables 6 and 7 show that within any given population-host combination, there is great variation. Chi-square tests (contingency tables) conducted on survival data showed that the populations are not significantly different ($P<.05$). There was no relationship between the response of clones to one host plant and their response to another host plant. For example, on alfalfa (Table 6), aphids of clone 2 from the early season sample of the alfalfa population were the heaviest aphids (0.86±.20 mg) while those of clone 9 were the lightest (0.54±.07 mg). But aphids of the same two clones were equal in weight on trefoil, weighing 0.39±.07 and 0.38±.13 respectively. On fababeans,

Table 6. Survival and mean adult dry weight (mg ± S.D.) of clones from various populations when reared on different hosts. (Early season - 1981)

Source of clones and hosts tested	No.* survived**	No. 1	No. 2	No. 3	No. 4	No. 5	No. 6	No. 7	No. 8	No. 9	No. 10
I. Clones from alfalfa population on hosts:											
Alfalfa	184	0.81±.10	0.86±.20	0.62±.10	0.79±.21	0.57±.10	0.65±.13	0.69±.17	0.82±.24	0.54±.07	0.76±.14
Trefoil	175	0.51±.14	0.39±.07	0.31±.06	0.44±.10	0.47±.10	0.39±.15	0.46±.11	0.48±.14	0.38±.13	0.44±.11
Fababeans	181	0.61±.14	0.46±.04	0.43±.06	0.60±.17	0.70±.15	0.77±.15	0.62±.15	0.66±.14	0.58±.11	0.64±.11
II. Clones from trefoil population on hosts:											
Alfalfa	169	0.26±.05	1.07±.22	0.59±.12	0.49±.11	0.64±.20	0.38±.12	0.40±.13	0.95±.10	0.57±.12	0.63±.12
Trefoil	175	0.51±.20	0.78±.14	0.37±.09	0.61±.15	0.25±.12	0.40±.10	0.31±.06	0.35±.07	0.46±.10	0.28±.06
Fababeans	181	0.51±.09	0.57±.11	0.55±.10	0.61±.14	0.47±.07	0.46±.09	0.45±.06	0.60±.17	0.60±.17	0.57±.07
III. Clones from sainfoin population on hosts:											
Alfalfa	176	0.71±.10	0.69±.09	0.81±.14	0.57±.12	0.47±.14	0.78±.19	0.77±.16	0.76±.12	0.77±.22	0.66±.23
Trefoil	158	0.39±.11	0.33±.10	0.28±.07	0.39±.08	0.34±.09	0.15±.04	0.36±.13	0.49±.10	0.31±.10	0.27±.03
Fababeans	190	0.72±.12	0.49±.19	0.53±.07	0.48±.10	0.52±.13	0.61±.14	0.61±.14	0.53±.10	0.67±.08	0.49±.05

*Number of nymphs that survived to the adult stage out of a total of 200 nymphs, 20 each from each clone, at the start of the experiment for each host.

**Number of nymphs that survived on sainfoin were 55, 37 and 52 for categories I, II and III respectively.

Table 7. Survival and mean adult dry weight (mg ± S.D.) of clones from various populations when reared on different hosts. (Late season - 1981)

Source of clones and hosts tested	No.* survived**	No. 1	No. 2	No. 3	No. 4	No. 5	No. 6	No. 7	No. 8	No. 9	No. 10
I. Clones from alfalfa population on hosts:											
Alfalfa	173	0.72±.21	0.73±.18	0.68±.14	0.58±.15	0.91±.07	0.42±.13	0.63±.16	0.65±.19	0.63±.11	0.68±.16
Trefoil	158	0.31±.08	0.33±.08	0.27±.05	0.64±.31	0.34±.09	0.28±.07	0.29±.02	0.28±.07	0.35±.06	0.37±.10
Fababeans	190	0.49±.07	0.56±.12	0.53±.13	0.47±.12	0.62±.15	0.56±.08	0.68±.11	0.55±.11	0.56±.09	0.58±.13
II. Clones from trefoil population on hosts:											
Alfalfa	152	0.63±.16	0.86±.18	0.28±.04	0.60±.12	0.53±.07	0.37±.07	0.84±.13	0.54±.13	0.27±.08	0.81±.19
Trefoil	164	0.29±.05	0.17±.02	0.24±.06	0.19±.02	0.42±.08	0.47±.09	0.30±.15	0.21±.09	0.26±.08	0.22±.04
Fababeans	180	0.63±.07	0.55±.06	0.54±.09	0.43±.06	0.59±.10	0.58±.16	0.52±.07	0.47±.13	0.40±.02	0.41±.11
III. Clones from sainfoin population on hosts:											
Alfalfa	126	-	-	-	0.46±	0.56±.09	-	0.36±.12	0.67±.12	0.68±.15	0.64±.19
Trefoil	157	0.29±.06	0.31±.07	0.44±.06	-	0.23±.04	0.30±.06	0.20±.09	0.25±.04	0.32±.03	0.13±.02
Fababeans	182	0.41±.08	0.40±.08	0.42±.06	0.45±.07	0.52±.11	0.71±.04	0.47±.02	0.67±.14	0.50±.04	0.45±.06

*Number of nymphs that survived to the adult stage out of a total of 200 nymphs, 20 each from each clone, at the start of the experiment for each host.

**Number of nymphs that survived on sainfoin were 44, 42 and 38 for categories I, II and III respectively.

their weights were not significantly different (0.46±.04 and 0.58±.11). Similarly on alfalfa, aphids of clone 2 of the early season sample of trefoil population were the heaviest (1.07±.22) while those of clone 1 were the lightest (0.26±.05), but on trefoil and fababeans the same two clones performed equally well. Clones 1 and 4 of the early season sample of the sainfoin population did not show any significant difference on hosts of alfalfa and trefoil while on fababeans their weights were significantly different (0.72±.12 and 0.48±.10 respectively). Similarly, clones 6 and 8 of the early season sample of the sainfoin population did not differ significantly on alfalfa and fababeans but on trefoil their weights were significantly different (0.15±.04 and 0.49±.10 respectively).

Likewise late season data (Table 7) show that within any given population-host combination there is great variation. When two particular clones are compared they perform equally on some hosts, but significantly differently on some other. Chi-square tests (contingency tables) show that survival of the clones from the alfalfa population on alfalfa (173) was significantly different from the clones of the sainfoin population (126) on alfalfa ($P<.05$). However, survival of the clones from the trefoil population on alfalfa (152) was not significantly different from those of the alfalfa population on alfalfa. Similarly on trefoil, survival of the clones from all three populations were not significantly different ($P>.05$). This suggests that the clones present on alfalfa later in the season are better adapted to alfalfa than the clones present on sainfoin are to alfalfa.

Based on the consistency exhibited by the 1980 clones over an

extended period of time, it seems likely that such measurements on clones are repeatable and hence are real.

(b) Fecundity

Fourth instar nymphs were caged on the four hosts (alfalfa, sainfoin, trefoil, and excised leaves of fababeans) and their fecundity was recorded every other day till the seventh day of reproduction. At each inspection the nymphs were removed and reared on excised fababean leaves in order to determine their morph. Tables 8 and 9 consist of data on fecundity of clones from populations sampled in early and late seasons respectively. Analysis of variance showed that samples from populations are not significantly different ($P>.05$) in fecundity. F ratio comparisons made between populations and between clones show that differences among clones between populations are no greater than differences among clones within any given population ($P>.01$). Fecundity data illustrate the fact that the host plant responses of one clone are unrelated to those of other clones. For instance, fecundities of aphids from clones 1 and 8 from the early season sample of the trefoil population (Table 8) on sainfoin and on fababeans are not significantly different while on trefoil and alfalfa fecundities are significantly different ($P<.05$). This type of clonal variation is apparent from Table 8 and 9 if two or three clones are compared together with regard to their fecundity on different hosts.

Late season data (Table 9) likewise indicate that there is a great deal of variation within any population-host combination, and two clones that perform similarly on one host can differ significantly in their per-

Table 8. Fecundity of clones from various populations on different hosts (± S.E.) (early season - 1981)

Source of clones and hosts tested	Mean progeny/female/seven days (± S.E.) (average of 10 replicates)									
	No. 1	No. 2	No. 3	No. 4	No. 5	No. 6	No. 7	No. 8	No. 9	No. 10
I. Clones from alfalfa population on hosts:										
Alfalfa	35.9±4.2^{ab}	49.6±7.8^{bc}	53.3±3.4^{c}	46.5±5.9^{ab}	35.3±8.5^{a}	59.1±4.3^{ab}	45.4±5.1^{a}	49.3±4.9^{c}	26.9±5.2^{ab}	52.3±5.0^{ab}
Sainfoin	7.7±3.2^{a}	3.7±3.0^{a}	6.7±3.0^{a}	3.6±1.0^{a}	4.5±8.4^{a}	0.0±0.0^{b}	5.6±11.1^{a}	6.1±4.9^{a}	0.3±0.0^{b}	1.2±1.0^{b}
Trefoil	9.4±8.8^{bc}	22.2±5.7^{a}	7.3±4.1^{bc}	7.5±7.7^{bc}	7.3±4.9^{bc}	14.8±4.9^{ab}	10.8±2.1^{ab}	27.4±6.0^{a}	1.5±2.1^{d}	6.5±6.5^{bc}
Fababeans	43.3±5.7^{a}	36.8±4.0^{c}	47.3±5.1^{ab}	49.2±5.1^{ab}	63.7±3.2^{a}	52.2±3.3^{ab}	50.6±10.5^{ab}	54.2±4.5^{ab}	25.5±3.7^{c}	44.7±4.4^{ab}
II. Clones from trefoil population on hosts:										
Alfalfa	6.5±6.7^{c}	55.2±5.5^{a}	25.0±6.5^{b}	21.6±4.1^{c}	38.5±7.0^{a}	28.1±3.4^{b}	26.2±7.0^{b}	30.6±4.9^{b}	35.1±5.8^{b}	34.2±10.4^{a}
Sainfoin	0.0±0.0^{a}	0.8±0.0^{a}	3.5±2.6^{a}	1.3±0.0^{a}	0.0±0.0^{a}	0.8±0.0^{a}	0.7±0.0^{a}	0.0±0.0^{a}	3.0±6.0^{a}	0.4±0.0^{a}
Trefoil	7.8±3.2^{c}	19.9±5.4^{bc}	7.3±4.0^{a}	15.1±2.3^{a}	6.9±6.0^{bc}	6.2±5.1^{bc}	12.8±2.3^{bc}	25.1±5.2^{ab}	7.2±3.7^{bc}	2.2±0.0^{d}
Fababeans	51.7±6.1^{a}	29.8±6.6^{b}	42.7±7.9^{a}	53.6±8.3^{a}	58.1±8.2^{a}	55.2±6.1^{a}	52.4±5.9^{a}	59.6±3.7^{a}	33.3±2.8^{a}	41.3±2.9^{a}
III. Clones from sainfoin population on hosts:										
Alfalfa	36.9±6.9^{c}	52.1±4.1^{a}	49.2±5.4^{a}	44.7±1.9^{b}	42.2±11.1^{a}	39.4±5.1^{a}	44.6±4.2^{b}	36.3±4.3^{a}	43.3±4.4^{a}	45.1±5.6^{a}
Sainfoin	0.0±0.0^{a}	0.1±0.0^{a}	0.0±0.0^{a}	0.0±0.0^{a}	0.1±0.0^{a}	2.8±3.0^{a}	0.0±0.0^{a}	0.9±2.5^{a}	0.0±0.0^{a}	5.4±4.5^{a}
Trefoil	23.8±5.4^{bcd}	7.4±5.1^{cd}	18.5±6.1^{abc}	17.8±2.5^{ab}	12.9±2.1^{abc}	18.0±3.5^{ab}	5.9±2.5^{d}	13.6±4.0^{bcd}	17.0±3.8^{a}	19.8±3.2^{abcd}
Fababeans	49.2±6.1^{a}	32.1±6.2^{a}	53.0±4.0^{a}	36.6±4.4^{a}	59.1±4.0^{ab}	29.7±1.9^{c}	30.6±2.7^{ab}	36.5±6.7^{ab}	60.6±1.6^{b}	39.2±3.2^{bc}

Analysis of variance and comparison of means were done on transformed $\sqrt{x}$ data.
Means followed by the same letter, within any given row, are not significantly different according to Duncan's multiple range test at the 5% level.

Table 9. Fecundity of clones from various populations on different hosts (± S.E.) (late season - 1981)

Source of clones and hosts tested	Mean progeny/female/seven days (± S.E.) (average of 10 replicates)									
	No. 1	No. 2	No. 3	No. 4	No. 5	No. 6	No. 7	No. 8	No. 9	No. 10
I. Clones from alfalfa population on hosts:										
Alfalfa	40.7 ± 6.2^{bc}	37.2 ± 7.8^{ab}	22.4 ± 8.1^{a}	43.7 ± 5.8^{abc}	52.7 ± 3.3^{bc}	46.8 ± 5.0^{a}	53.6 ± 9.8^{abc}	32.2 ± 9.8^{ab}	48.1 ± 6.5^{c}	39.4 ± 5.7^{a}
Sainfoin	0.3 ± 0.0^{b}	0.0 ± 0.0^{b}	0.5 ± 0.0^{b}	2.1 ± 1.3^{a}	0.6 ± 0.0^{b}	0.0 ± 0.0^{b}	0.0 ± 0.0^{b}	0.8 ± 0.0^{b}	8.1 ± 3.5^{a}	0.0 ± 0.0^{b}
Trefoil	9.2 ± 3.4^{bc}	1.1 ± 0.5^{ab}	4.9 ± 3.4^{cd}	7.0 ± 2.5^{bcd}	2.4 ± 1.1^{cd}	7.1 ± 1.7^{abc}	1.9 ± 3.5^{abc}	4.5 ± 3.1^{a}	26.7 ± 3.6^{d}	10.4 ± 2.5^{cd}
Fababeans	55.8 ± 2.0^{ab}	45.2 ± 2.0^{bc}	34.8 ± 5.5^{ab}	37.7 ± 5.6^{ab}	33.5 ± 4.7^{a}	35.2 ± 5.9^{ab}	34.8 ± 5.3^{abc}	40.0 ± 3.9^{ab}	43.2 ± 6.3^{c}	28.8 ± 3.4^{ab}
II. Clones from trefoil population on hosts:										
Alfalfa	11.6 ± 7.4^{d}	2.0 ± 0.0^{bc}	10.7 ± 3.3^{bc}	54.6 ± 4.2^{bc}	48.3 ± 6.4^{ab}	37.9 ± 9.8^{abc}	21.7 ± 5.8^{cd}	33.7 ± 6.2^{abc}	25.7 ± 9.8^{abc}	1.6 ± 0.0^{bcd}
Sainfoin	0.2 ± 0.0^{a}	0.0 ± 0.0^{a}	1.8 ± 3.5^{a}	1.9 ± 5.0^{a}	0.0 ± 0.0^{a}	0.8 ± 0.0^{a}	1.1 ± 0.0^{a}	3.6 ± 2.4^{a}	0.0 ± 0.0^{a}	0.0 ± 0.0^{a}
Trefoil	10.6 ± 5.8^{cd}	8.7 ± 2.3^{a}	30.5 ± 2.3^{bcd}	28.8 ± 4.7^{abc}	15.1 ± 6.2^{cd}	9.5 ± 2.1^{bcd}	13.0 ± 2.7^{ab}	14.9 ± 1.9^{a}	12.0 ± 2.8^{bcd}	0.0 ± 0.0^{d}
Fababeans	47.1 ± 3.0^{ab}	34.9 ± 2.5^{c}	45.7 ± 11.5^{ab}	54.0 ± 9.6^{ab}	46.5 ± 4.6^{a}	41.9 ± 4.5^{a}	43.0 ± 4.2^{ab}	32.5 ± 3.9^{a}	28.2 ± 5.9^{bc}	6.3 ± 1.3^{bc}
III. Clones from sainfoin population on hosts:										
Alfalfa	1.5 ± 6.5^{b}	0.1 ± 0.0^{b}	40.9 ± 3.6^{ab}	11.3 ± 7.6^{ab}	49.2 ± 2.7^{ab}	15.6 ± 12.2^{ab}	51.6 ± 2.4^{ab}	68.6 ± 5.0^{a}	55.7 ± 4.3^{a}	38.2 ± 4.3^{ab}
Sainfoin	0.0 ± 0.0^{b}	0.2 ± 0.0^{b}	0.3 ± 0.5^{b}	0.0 ± 0.0^{b}	1.2 ± 1.0^{ab}	0.0 ± 0.0^{b}	0.1 ± 0.0^{b}	5.8 ± 2.1^{a}	0.3 ± 0.5^{b}	0.0 ± 0.0^{b}
Trefoil	7.6 ± 3.7^{a}	3.4 ± 1.2^{b}	9.0 ± 2.1^{a}	14.8 ± 3.5^{a}	14.0 ± 2.7^{ab}	14.9 ± 2.9^{a}	4.4 ± 3.8^{b}	8.4 ± 3.5^{ab}	21.0 ± 1.5^{a}	8.3 ± 1.2^{a}
Fababeans	56.6 ± 7.9^{abc}	49.2 ± 6.5^{c}	15.9 ± 2.4^{bc}	54.7 ± 7.0^{bc}	30.6 ± 2.7^{ab}	51.0 ± 7.9^{c}	34.0 ± 5.6^{c}	35.8 ± 7.0^{c}	40.8 ± 6.3^{a}	19.8 ± 5.8^{abc}

Analysis of variance and comparison of means were done on transformed log (x + 1) data.
Means followed by the same letter, within any given row, are not significantly different according to Duncan's multiple range test at the 5% level.

formance on another host. Similarly, two clones which behave equally on one host with regard to one measure can differ on the same host with regard to another measure. For instance, dry weights of aphids from clones 3 (0.44±.06) and clone 5 (0.23±.04) from the late season sample of the sainfoin population tested on trefoil (Table 7) are significantly different whereas their fecundity on the same host (9.0 and 14.0 respectively) are not significantly different ($P>.05$) (Table 9). Similarly, mean fecundity of aphids from clones 3 (15.9) and clone 9 (40.8) from the late season sample of sainfoin population tested on fababeans differ significantly (Table 9) while their dry weights (0.42±.06 and 0.50±.04) are not significantly different (Table 7). This phenomenon was clearly exhibited by the three 1980 clones with regard to their fecundity and dry weights on fababeans as well as their responses to a crowding stimulus (Table 4, 5 and Figure 9).

Analysis of variance comparing early and late season fecundity data indicates that the responses of clones collected during the two seasons differ significantly ($P<.005$). Table 10 represents progeny production on alfalfa by clones sampled from different populations during early and late seasons. It reveals that total fecundity of clones sampled from the alfalfa population on alfalfa declined from early to late season by 8.1% as against 16.9% for clones sampled from the trefoil population on alfalfa and 23.3% for clones sampled from the sainfoin population on alfalfa. Orthogonal comparisons made on these data indicate that the reductionsof total fecundity of clones sampled from the alfalfa population on alfalfa (8.1%) is not significant whereas reductionsin progeny of clones sampled from the trefoil population (16.9%) and that of clones

Table 10. Progeny production by clones from different populations during early and late seasons - 1981

Clones sampled from populations on:	Total progeny on alfalfa by 10 clones with 10 replicates			Total progeny on trefoil by 10 clones with 10 replicates		
	Early season	Late season	% increase or decrease from early to late	Early season	Late season	% increase or decrease from early to late
Alfalfa	4536	4168	8.1 ↓	1147	752	34.4 ↓
Trefoil	2932	2478	16.9 ↓	1108	1431	29.1 ↑
Sainfoin	4338	3327	23.3 ↓	1547	1058	31.6 ↓

sampled from the sainfoin population (23.3%) are significant ($P<.05$). Similarly, Table 10 also represents total progeny of clones sampled from different populations, early and late, on trefoil. Clones sampled from the alfalfa population show a reduction of progeny from early to late season by 34.4% while the number of progeny of clones sampled from the trefoil population increased by 29.2%. Clones sampled from the sainfoin population recorded a decrease on trefoil of 31.6% from early to late season. Orthogonal comparisons made on these data indicate that this increase in fecundity by 29.2% is significant ($P<.01$). This indicates that the clones sampled from the trefoil population show some improved performance over the season when tested on trefoil, while the clones sampled from the other two populations show reduced performance when tested on trefoil.

Out of the 63 clones tested in 1980 and 1981, only one clone was found to perform well on sainfoin. This clone had been collected on alfalfa during the latter part of the season in 1981, and was retained and tested further. These data revealed that this clone produced an average of 39.4 progeny/female on sainfoin during its first 10 days of reproduction. This was the highest fecundity figure recorded on sainfoin by any clone during the present study. It produced 8.8% alatae on sainfoin.

(c) Alata Production

Pooled data on alata production by different clones measured during the 1981 studies are presented in Table 11. In the early season, clones sampled from the alfalfa and trefoil populations exhibited no

Table 11. Production of alatae by clones from different populations sampled in 1981 (± S.E.)

Clones sampled from	Early season* % alatae	Late season** % alatae
	I. On alfalfa	
Alfalfa	0.0 (N: - 1724)	0.0 (N: - 1598)
Trefoil	0.55 (N: - 1149)	8.35±2.37 (N: - 1098)
	II. On trefoil	
Alfalfa	1.49±1.23 (N: - 659)	15.65±0.97 (N: - 555)
Trefoil	1.96±1.29 (N: - 728)	1.42±1.23 (N: - 936)

*Based on ten clones from each field collected on 09 June 1981.

**Based on ten clones from each field collected on 29 July 1981.

N is the total individuals monitored.

alata production on either alfalfa or trefoil. However, later in the season, clones sampled from the trefoil population showed increased production of alata on alfalfa but not on trefoil. The clones sampled from the alfalfa population produced increased numbers of alatae on trefoil but not on alfalfa. Chi-square tests (contingency tables) conducted on these data show significant differences ($P<.05$). These data suggest that these populations show some differential selection on their respective hosts towards the latter part of the season.

iii. 1982 clones

(a) Fecundity

Procedures followed were the same as in the 1981 experiments except that in addition to alfalfa (var. Beaver), alfalfa (var. Algonquin) was included as a host while sainfoin was excluded. Sainfoin appeared to be a very poor host on which most of the clones did not reproduce at all. Samples of clones to be tested were collected only from the fields of two alfalfa varieties mentioned above but the alfalfa (var. Beaver) field here was different from that of 1981 collection. Table 12 consists of fecundity data for clones sampled from the populations early in the season while Table 13 includes for those clones sampled from the populations later in the season. As in 1981, two clones which behave similarly on one host may behave differently on another. For instance, clones 3 and 4 collected in the early season from the alfalfa (var. Algonquin) population tested on alfalfa (var. Algonquin) (Table 12) differed significantly at $P<.05$ (18.8 and 57.1 progeny/female respec-

Table 12. Fecundity of clones from various populations on different hosts (± S.E.) (early season - 1982)

Source of clones and hosts tested	Mean progeny/female/seven days (± S.E.) (average of 10 replicates)											
	No. 1	No. 2	No. 3	No. 4	No. 5	No. 6	No. 7	No. 8	No. 9	No. 10	No. 11	No. 12
I. Clones from alfalfa (var. Algonquin) population on hosts:												
Alfalfa (var. Algonquin)	$26.6_{\pm 6.1}^{cd}$	$45.9_{\pm 1.7}^{b}$	$18.8_{\pm 8.3}^{d}$	$57.1_{\pm 3.1}^{ab}$	$34.2_{\pm 10.1}^{bc}$	$44.5_{\pm 3.6}^{b}$	$30.7_{\pm 5.7}^{cd}$	$46.1_{\pm 8.6}^{b}$	$35.7_{\pm 2.9}^{bc}$	$59.5_{\pm 3.2}^{a}$	$34.7_{\pm 3.3}^{bc}$	$46.0_{\pm 3.3}^{b}$
Alfalfa (var. Beaver)	$38.8_{\pm 1.8}^{bc}$	$46.6_{\pm 3.2}^{ab}$	$39.1_{\pm 6.0}^{bc}$	$56.3_{\pm 2.0}^{a}$	$57.8_{\pm 4.3}^{a}$	$47.8_{\pm 4.7}^{ab}$	$50.1_{\pm 3.0}^{ab}$	$54.5_{\pm 6.0}^{a}$	$37.3_{\pm 4.5}^{bcd}$	$31.1_{\pm 3.3}^{d}$	$31.2_{\pm 4.1}^{cd}$	$24.2_{\pm 4.2}^{d}$
Trefoil	$22.0_{\pm 2.1}^{a}$	$13.0_{\pm 4.3}^{abc}$	$21.9_{\pm 2.0}^{a}$	$6.6_{\pm 3.3}^{c}$	$11.5_{\pm 2.8}^{abc}$	$16.6_{\pm 4.5}^{ab}$	$1.1_{\pm 0.5}^{c}$	$18.2_{\pm 2.6}^{ab}$	$14.6_{\pm 2.8}^{ab}$	$14.1_{\pm 2.4}^{abc}$	$7.3_{\pm 3.3}^{bc}$	$18.4_{\pm 3.2}^{ab}$
Fababeans	$53.8_{\pm 1.0}^{ab}$	$56.1_{\pm 1.1}^{a}$	$52.9_{\pm 4.8}^{ab}$	$60.8_{\pm 2.3}^{a}$	$47.1_{\pm 5.7}^{abc}$	$36.9_{\pm 4.5}^{cd}$	$48.2_{\pm 2.2}^{abc}$	$32.0_{\pm 6.3}^{d}$	$46.7_{\pm 4.8}^{bc}$	$41.2_{\pm 4.1}^{bcd}$	$31.6_{\pm 2.2}^{d}$	$38.6_{\pm 4.2}^{cd}$
II. Clones from alfalfa (var. Beaver) population on hosts:												
Alfalfa (var. Algonquin)	$32.6_{\pm 7.3}^{ab}$	$14.0_{\pm 5.8}^{c}$	$30.6_{\pm 1.9}^{ab}$	$25.1_{\pm 6.0}^{bc}$	$33.8_{\pm 3.3}^{ab}$	$39.7_{\pm 5.7}^{a}$	$13.5_{\pm 3.5}^{c}$	$39.6_{\pm 6.2}^{a}$	$29.2_{\pm 9.8}^{ab}$	$35.6_{\pm 2.6}^{ab}$	$22.2_{\pm 3.8}^{bc}$	$41.9_{\pm 4.6}^{a}$
Alfalfa (var. Beaver)	$58.5_{\pm 2.2}^{a}$	$36.0_{\pm 5.5}^{cd}$	$40.8_{\pm 4.2}^{bc}$	$24.6_{\pm 2.9}^{def}$	$24.5_{\pm 3.8}^{def}$	$21.4_{\pm 6.4}^{ef}$	$31.0_{\pm 4.3}^{cde}$	$51.5_{\pm 3.7}^{ab}$	$37.2_{\pm 5.7}^{cd}$	$15.1_{\pm 4.3}^{f}$	$36.4_{\pm 5.7}^{cd}$	$40.5_{\pm 3.6}^{bc}$
Trefoil	$38.7_{\pm 3.5}^{a}$	$22.0_{\pm 6.7}^{bcd}$	$33.0_{\pm 1.5}^{ab}$	$8.5_{\pm 2.4}^{e}$	$14.7_{\pm 1.8}^{de}$	$11.0_{\pm 2.1}^{de}$	$29.2_{\pm 1.9}^{abc}$	$18.4_{\pm 4.9}^{cd}$	$16.1_{\pm 2.7}^{cde}$	$15.2_{\pm 4.4}^{de}$	$4.4_{\pm 1.7}^{e}$	$14.1_{\pm 3.7}^{de}$
Fababeans	$54.4_{\pm 1.9}^{a}$	$44.8_{\pm 1.8}^{ab}$	$26.3_{\pm 3.8}^{cde}$	$21.3_{\pm 3.9}^{def}$	$34.9_{\pm 3.2}^{bcd}$	$12.1_{\pm 1.5}^{f}$	$27.2_{\pm 4.3}^{cde}$	$35.4_{\pm 4.3}^{bc}$	$25.4_{\pm 4.7}^{cdef}$	$14.1_{\pm 1.7}^{ef}$	$24.3_{\pm 3.5}^{cdef}$	$21.5_{\pm 3.2}^{def}$

Means followed by the same letter, within any given row, are not significantly different according to Duncan's multiple range test at the 5% level.

Table 13. Fecundity of clones from various populations on different hosts (± S.E.) (late season - 1982)

Source of clones and hosts tested	Mean progeny/female/seven days (± S.E.) (average of 10 replicates)											
	No. 1	No. 2	No. 3	No. 4	No. 5	No. 6	No. 7	No. 8	No. 9	No. 10	No. 11	No. 12
I. Clones from alfalfa (var. Algonquin) population on hosts:												
Alfalfa (var. Algonquin)	50.4 ±3.3 bcd	41.4 ±7.2 de	64.7 ±1.7 a	51.4 ±4.4 bcd	56.0 ±4.0 abc	33.0 ±7.5 e	32.6 ±5.9 e	44.9 ±5.9 cde	43.9 ±5.9 cde	40.1 ±5.0 de	61.1 ±6.4 ab	33.6 ±10.3 e
Alfalfa (var. Beaver)	41.8 ±6.2 ab	20.3 ±5.2 c	54.4 ±2.3 a	44.9 ±6.3 ab	46.7 ±1.8 a	50.1 ±3.1 a	32.5 ±4.2 bc	50.9 ±1.7 a	43.4 ±3.9 ab	45.3 ±2.2 ab	47.0 ±4.2 a	47.9 ±8.0 a
Trefoil	24.1 ±2.8 abc	17.7 ±4.1 bcd	12.6 ±2.2 cd	15.7 ±2.7 cd	7.7 ±1.4 d	34.8 ±3.3 a	23.0 ±1.7 abc	17.5 ±2.7 bcd	24.0 ±2.2 abc	21.3 ±2.3 abc	29.9 ±2.9 ab	29.1 ±3.9 ab
Fababeans	40.1 ±3.7 b	51.2 ±1.7 ab	46.7 ±1.5 ab	46.4 ±1.3 ab	45.1 ±1.1 ab	43.4 ±2.3 ab	41.2 ±1.1 b	46.0 ±0.9 ab	49.3 ±2.2 ab	46.2 ±3.2 ab	38.8 ±3.9 b	54.6 ±1.5 a
II. Clones from alfalfa (var. Beaver) population on hosts:												
Alfalfa (var. Algonquin)	21.0 ±4.9 bc	35.8 ±4.4 a	21.8 ±4.6 bc	15.0 ±4.6 c	14.1 ±9.6 c	32.2 ±7.6 ab	40.0 ±6.5 a	19.9 ±5.3 bc	14.8 ±4.0 c	15.1 ±4.9 c	31.0 ±4.4 ab	12.8 ±2.4 c
Alfalfa (var. Beaver)	39.4 ±7.3 cde	62.5 ±5.2 a	27.3 ±1.9 ef	39.4 ±2.7 cde	46.9 ±6.6 bc	58.6 ±5.6 ab	42.1 ±5.0 cd	45.0 ±4.3 bc	37.5 ±5.2 cdef	31.3 ±4.5 def	24.9 ±3.2 f	37.4 ±4.1 cdef
Trefoil	16.8 ±3.3 ab	26.3 ±5.4 a	10.8 ±1.8 b	18.8 ±3.4 ab	20.5 ±3.0 ab	24.3 ±3.4 a	14.1 ±3.1 ab	23.7 ±4.2 ab	11.6 ±2.2 b	13.4 ±2.4 ab	10.8 ±1.8 b	16.6 ±2.2 ab
Fababeans	50.0 ±1.9 ab	55.9 ±2.5 a	25.4 ±1.9 d	40.4 ±4.1 bc	64.4 ±3.5 a	50.0 ±2.9 ab	28.7 ±1.8 cd	34.4 ±4.9 cd	33.1 ±5.6 cd	27.1 ±4.2 cd	25.4 ±4.4 d	29.7 ±4.6 cd

Means followed by the same letter, within any given row, are not significantly different according to Duncan's multiple range test at the 5% level.

tively), but their performance was not different on fababeans (52.9 and 60.8 progeny/female respectively). However, on trefoil, the same clones 3 and 4 had 21.9 and 6.6 progeny/female respectively and also on alfalfa (var. Beaver) they had 39.1 and 53.3 progeny/female respectively. These figures differ significantly ($P<.05$). Late season data (Table 13) also exhibit the same phenomenon. For instance, clones 5 and 7 which were sampled from the alfalfa (var. Beaver) population, when tested on alfalfa (var. Algonquin) had mean progeny/female of 14.1 and 40.0 respectively. These figures differ significantly ($P<.05$). But on alfalfa (Beaver) and trefoil their differences were not significant. On fababeans they differed significantly with 64.4 progeny/female being produced by clone 5 and only 28.7 progeny/female by clone 7.

An analysis of variance done on early and late season samples, comparing fecundities indicates that early and late clones sampled from different populations differ significantly ($P<.005$). Table 14 shows progeny production on alfalfa (var. Algonquin) by clones sampled from different populations during early and late seasons. This indicates that clones sampled from the alfalfa (var. Beaver) exhibited decrease in total progeny production of 23.6% on alfalfa (var. Algonquin) from early to late season, while clones sampled from alfalfa (var. Algonquin) on the host alfalfa (var. Algonquin) increased by 15.3%. These two figures are significantly different ($P<.01$). Similarly, clones sampled from the alfalfa (var. Beaver) population tested on the host alfalfa (var. Beaver) (Table 14) had an increase in progeny production of 20.1% as compared with only 2.0% increase by clones sampled from the alfalfa

Table 14. Progeny production by clones from different populations during early and late seasons - 1982

Clones sampled from populations on:	Total progeny on alfalfa (var. Algonquin) by 12 clones with 10 replicates			Total progeny on alfalfa (var. Beaver) by 12 clones with 10 replicates		
	Early season	Late season	% increase or decrease from early to late	Early season	Late season	% increase or decrease from early to late
Alfalfa (var. Beaver)	3578	2735	23.6 ↓	4175	5013	20.1 ↑
Alfalfa (var. Algonquin)	4797	5531	15.3 ↑	5147	5252	2.0 ↑

(var. Algonquin) population tested on alfalfa (Beaver). This indicates that the clones from the alfalfa (var. Beaver) population show better adaptation on alfalfa (var. Beaver) over the season than the clones from the other variety. Similarly, the clones from the alfalfa (var. Algonquin) population tested on alfalfa (var. Algonquin) show better adaptation to that host than the set of clones sampled from the alfalfa (var. Beaver) population.

The 1982 studies conducted led to other findings. The sample of 12 clones collected in early season from the alfalfa (var. Algonquin) population differed from the sample of 12 clones collected early season from the alfalfa (var. Beaver) population with regard to their fecundity on the two varieties of alfalfa ($P<.05$). This was the only case in which populations were significantly different. The late season sample of 12 clones from each population were also significantly different ($P<.05$) from each other with regard to their fecundity. There were several differences between these populations. The alfalfa (var. Algonquin) field was 6 years old while the alfalfa (var. Beaver) field was four years old. The alfalfa (var. Beaver) field was situated south of the city of Winnipeg and had been used for hay. The alfalfa (var. Algonquin) field was located Northeast of the city and had been used for seed production. The distance between the fields was about 50 km. In addition, insecticides had been used every year on the alfalfa (var. Algonquin) field. This might have acted as a strong selection pressure on the aphid populations. The alfalfa (var. Beaver) field had received no insecticides at all.

The clones from the alfalfa (var. Algonquin) population showed increased fecundity compared with those from alfalfa (var. Beaver).

For instance, 12 clones sampled in the early season from the alfalfa (var. Algonquin) population produced 4797 progeny on alfalfa (var. Algonquin) as against 3578 progeny by the 12 clones from the alfalfa (var. Beaver) population on the same host. Likewise, the same 12 clones from the alfalfa (var. Algonquin) population produced 5147 progeny on alfalfa (var. Beaver) as against 4175 progeny by the corresponding 12 clones from the alfalfa (var. Beaver) population (Table 14). Late collected samples showed even greater differences. In late collected samples of 12 clones from the alfalfa (var. Algonquin) population had 5531 progeny on alfalfa (var. Algonquin) as against 2735 progeny by the 12 clones sampled from the alfalfa (var. Beaver) population on the same host (Table 14). This increased fecundity in alfalfa (var. Algonquin) clones could be due to several factors. Higher average fitness caused by the selection pressure of the insecticidal treatment could be one factor. However, the effects of variety, field age, and locations cannot be excluded at this time.

Table 15 consists of data on mean progeny of early and late collected clones from the alfalfa (var. Algonquin) population on all the four hosts tested in the laboratory. This shows that the twelve clones collected later in the season in 1982 did not exhibit significant clonal variability ($P>.05$), whereas early collected clones did so.

(b) Alata Production

Table 16 shows the pooled data on alata production. Here again, early sampled clones from different populations show no marked difference in their alata production on any host. However, the clones

Table 15. Variability* of clones from the alfalfa (var. Algonquin) population during early and late seasons (1982)

Clones collected early season	1ab (35.5)	2a (40.4)	3ab (33.2)	4ab (33.1)	5ab (37.7)	6ab (36.5)	7ab (32.5)	8ab (37.7)	9ab (33.6)	10ab (36.5)	11b (26.2)	12ab (31.8)
Clones collected late season	1a (39.1)	2a (32.7)	3a (44.6)	4a (39.6)	5a (38.9)	6a (40.3)	7a (32.3)	8a (39.8)	9a (40.2)	10a (38.2)	11a (44.2)	12a (41.3)

*Based on mean progeny on all the four hosts (fababeans, trefoil, alfalfa (var. Algonquin) and alfalfa (var. Beaver) tested in the laboratory.
Numbers with the same letters within any given row are not significantly different ($P<.05$) according to Duncan's multiple range test.
Figures within parenthesis are mean progeny/female/seven days, average of ten replicates.

Table 16. Production of alatae by clones from different populations sampled in 1982 (± S.E.)

Clones sampled from	Early season* % alatae	Late season** % alatae
	I. On alfalfa (var. Algonquin)	
Alfalfa (var. Algonquin)	0.35 (N: - 1413)	0.0 (N: - 1519)
Alfalfa (var. Beaver)	0.0 (N: - 1218)	6.57±1.91 (N: - 928)
	II. On alfalfa (var. Beaver)	
Alfalfa (var. Algonquin)	0.18 (N: - 1667)	4.50±1.91 (N: - 1378)
Alfalfa (var. Beaver)	0.0 (N: - 1091)	0.06 (N: - 1570)

*Based on 12 clones each collected from alfalfa (var. Algonquin) on 30 May 1982, and from alfalfa (var. Beaver) on 28 May 1982.

**Based on 12 clones each collected from alfalfa (var. Algonquin) on 16 July 1982, and from alfalfa (var. Beaver) on 30 July 1982.

N is the total individuals monitored.

sampled later in the season from the alfalfa (var. Beaver) population showed increased production of alata (6.57%) on alfalfa (var. Algonquin) but not on (var. Beaver), while the clones sampled from the alfalfa (var. Algonquin) produced alata on alfalfa (var. Beaver) but not on alfalfa (var. Algonquin). Chi-square tests (contingency tables) done on these data show significant differences ($P<.05$). These data indicate that these populations show some differential selection towards the later part of the season.

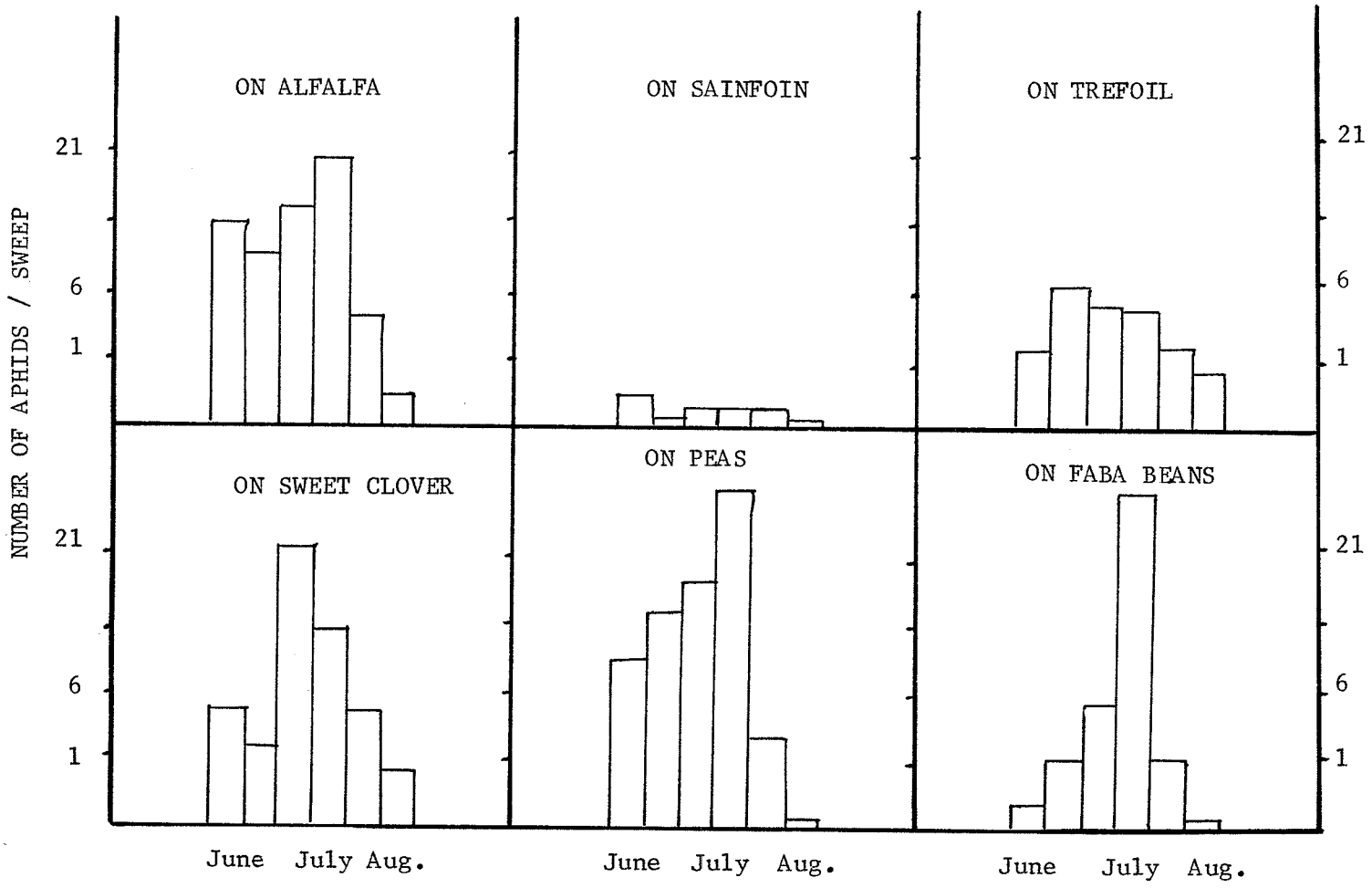
3. Field Studies

In 1980, there were no aphids available on crops during the early part of the field season at the Research Station, Glenlea. The 1980 drought had adverse effects on all crop production in Manitoba (Phillips 1980). On the six crops (alfalfa, sainfoin, trefoil, sweet clover, peas and fababeans) seeded in early May, 1980, aphids did not appear until early July, after which time there was a sudden increase in aphid populations. Therefore field studies could not be initiated until July, 1980.

In 1981, aphids appeared on crops in late May and were consistently present until mid-August, after which they declined to low levels (Figure 10). In addition to the laboratory studies, field studies were carried out throughout this period. In 1982, field-collected samples of aphids were tested in the laboratory because of the easier and more precise handling possible in the laboratory compared with the field.

Based on the work conducted in 1980 and 1981, sainfoin was found to be a very poor host on which most of the aphids showed high mortality.

Figure 10. Field populations in 1981 (June through August) (Number of aphids/sweep; Average of 50 sweep/host).


ON ALFALFA
ON SAINFOIN
ON TREFOIL
ON SWEET CLOVER
ON PEAS
ON FABA BEANS
NUMBER OF APHIDS / SWEEP
21
6
1
June
July
Aug.

Therefore, sainfoin was excluded as a host in 1982 experiments. Field transfers were made (1980 and 1981) among fields of alfalfa, sainfoin, trefoil, sweet clover, peas and fababeans. These were replicated 12 times in 1980, 20 times in 1981 at variable intervals over the season, and eight times in 1982.

Data on fecundity are presented in Figure 11 for aphids sampled from populations on perennials during the three years. Figure 12 represents the data on survival to reproduction while Figure 13 represents the fecundity data for aphids sampled from populations on annuals over the three years.

Data on field populations on different hosts from June through August, 1981, (Figure 10) show that field population data followed the same trend of preference as exhibited by the data for field experiments, i.e. peas, alfalfa, sweet clover, fababeans, trefoil and sainfoin in descending order.

Analysis of variance was done separately on the data from each year. There were no significant differences ($P>.01$) among samples of populations tested with regard to their fecundity. Chi-square tests (contingency tables) conducted with data on survival to reproduction (Figure 12) also confirms that the populations are not significantly different ($P>.01$). Analysis of variance also indicates that the responses to various hosts by aphids differ significantly ($P<.01$) while host-population interaction is significant ($P<.01$). As shown in the laboratory studies, this also shows that the characteristics of different populations are not distinct as they are made up of widely

Figure 11. Fecundity of aphids sampled from different populations on perennials and when reared on different hosts in the field.

Analysis of variance and comparison of means were done on transformed $\sqrt{X}$ data in 1980, $X^{.28}$ data in 1981, and $X^{.1}$ data in 1982.

The same letters above the bars, within any given population-host combination indicate no significant differences among the hosts according to Duncan's multiple range test at the 5% level.

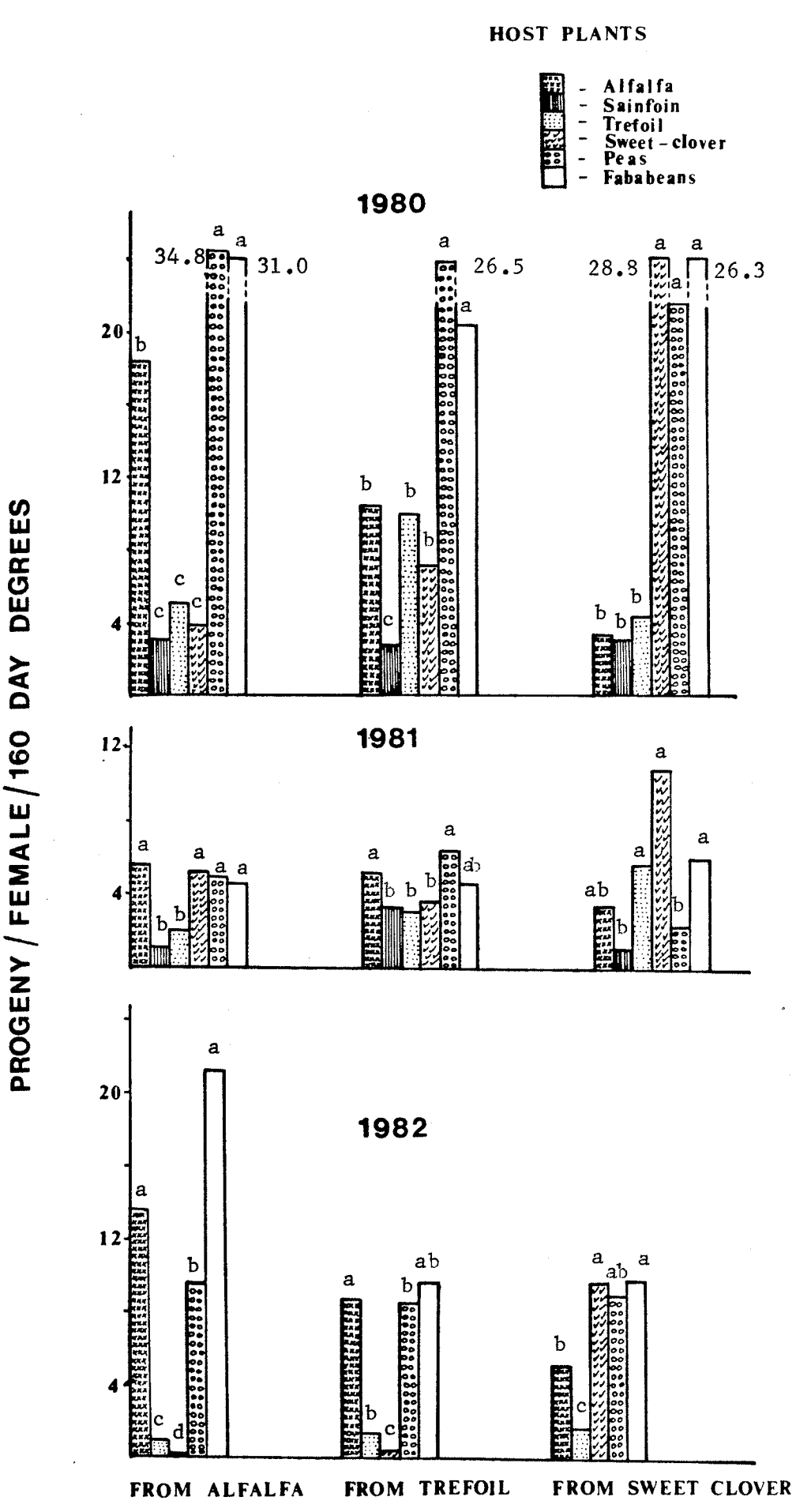

HOST PLANTS
- Alfalfa
- Sainfoin
- Trefoil
- Sweet - clover
- Peas
- Fababeans
1980
34.8
31.0
26.5
28.8
26.3
1981
1982
PROGENY / FEMALE / 160 DAY DEGREES
20
12
4
FROM ALFALFA
FROM TREFOIL
FROM SWEET CLOVER

Figure 12. Survival to reproduction of aphids sampled from populations on perennials and when caged on different hosts in the field.

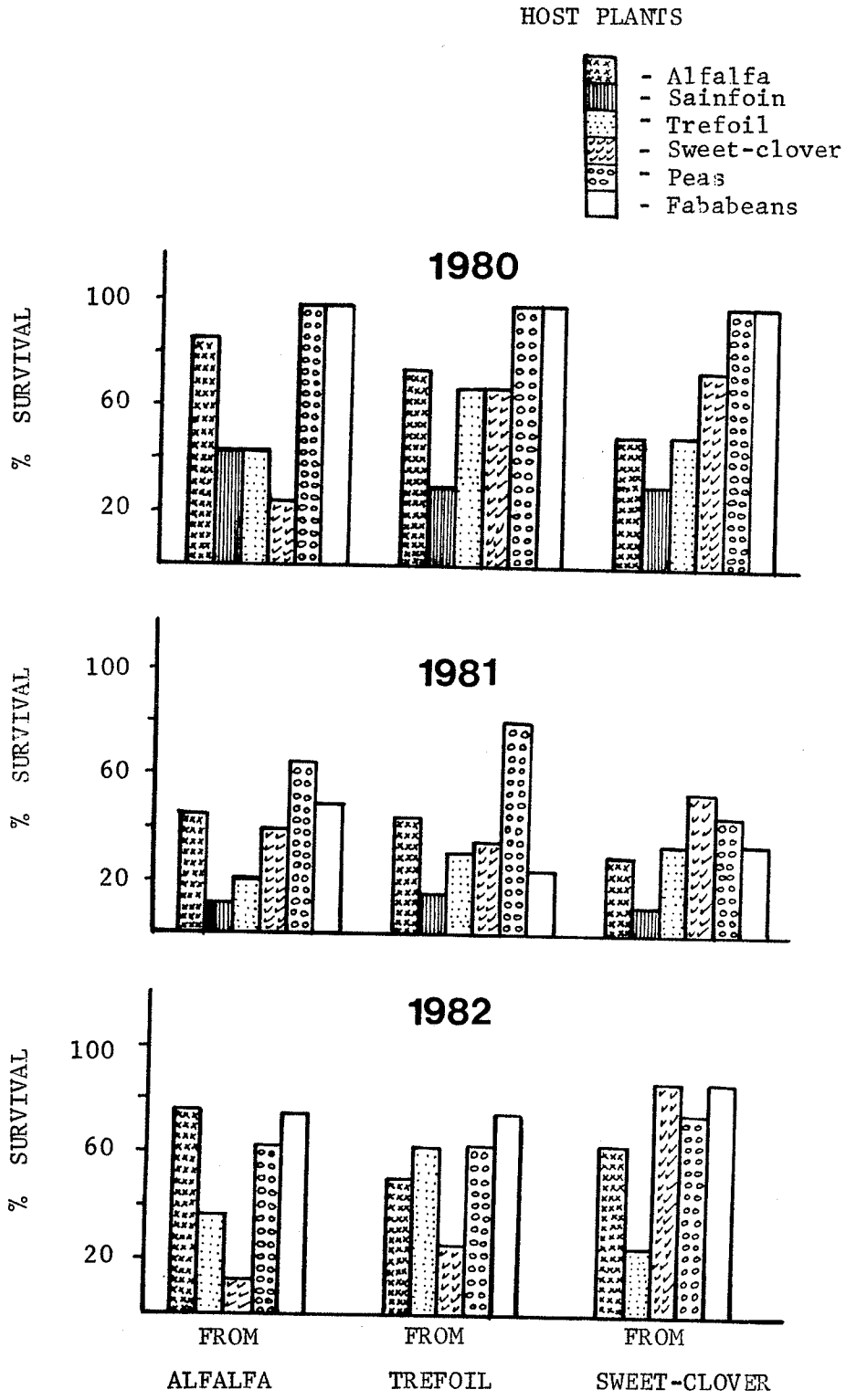
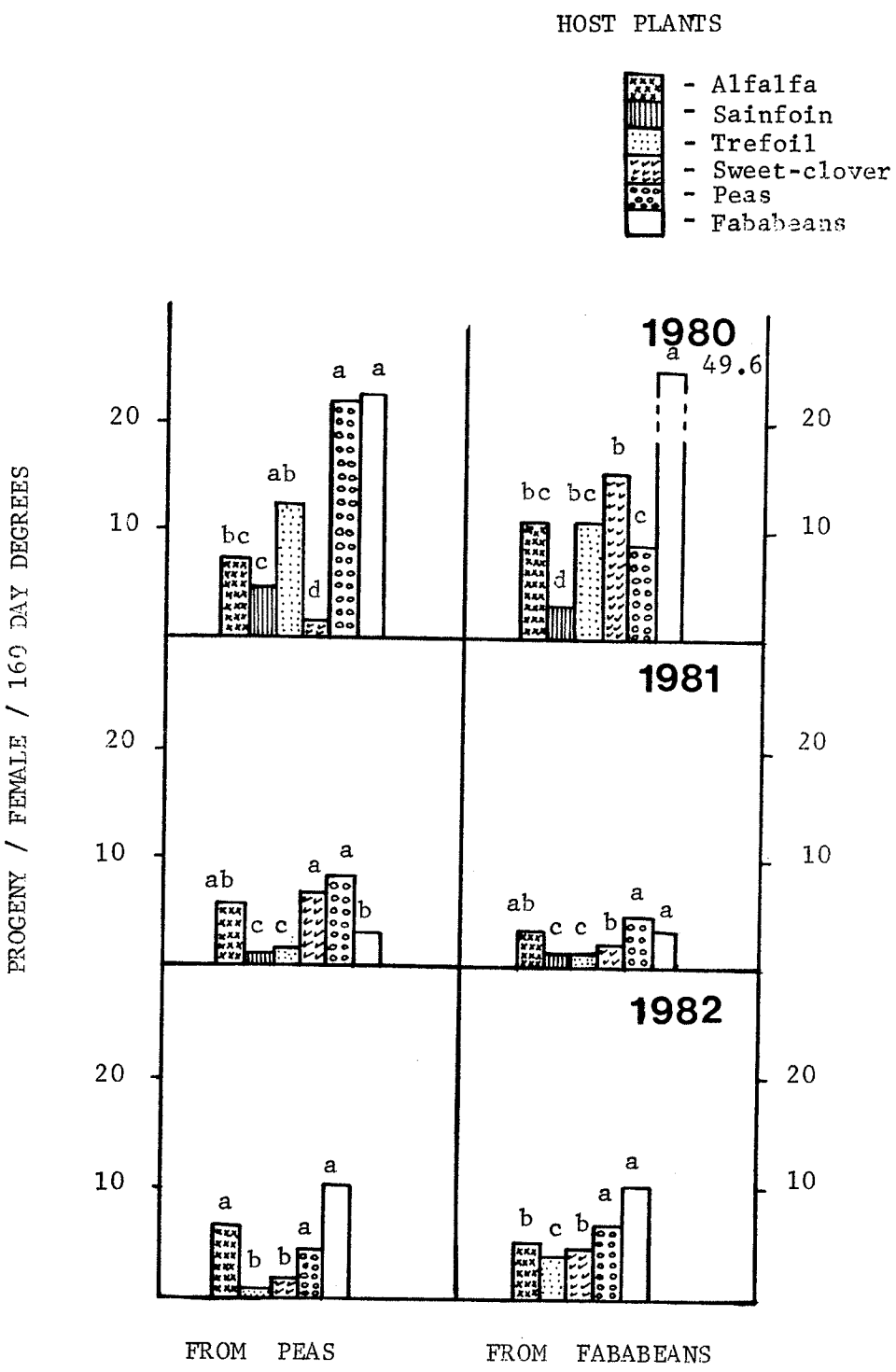

HOST PLANTS
- Alfalfa
- Sainfoin
- Trefoil
- Sweet-clover
- Peas
- Fababeans
1980
1981
1982
% SURVIVAL
100
60
20
FROM ALFALFA
FROM TREFOIL
FROM SWEET-CLOVER

Figure 13. Fecundity of aphids sampled from populations on annuals and when reared on different hosts in the field.

Analysis of variance and comparison of means were done on transformed $\log(X + 1)$ data.
The same letters above the bars, within any given population-host combination indicate no significant differences according to Duncan's multiple range test at the 5% level.


HOST PLANTS
- Alfalfa
- Sainfoin
- Trefoil
- Sweet-clover
- Peas
- Fababeans
1980
1981
1982
49.6
PROGENY / FEMALE / 160 DAY DEGREES
20
10
FROM PEAS
FROM FABABEANS

different genotypes, with no relationship between the responses of clones within any given population to one host plant and their responses to another host plant.

Aphids from all the populations generally did well on the two annuals (peas and fababeans) with the exception that aphids from the fababeans population did poorly on peas in 1980 (Figure 13), and aphids from the sweet clover population did poorly on peas in 1981 (Figure 11). But these differences were not found in other years.

In 1980, aphids from the alfalfa population had significantly different ($P<.05$) fecundity on alfalfa versus sweet clover. However, their differences were not significant in 1981 while in 1982 they were again found to be significant ($P<.05$). Aphids from the trefoil population did equally well on trefoil and alfalfa in 1980, but in 1981 and 1982 were significantly different ($P<.05$). Likewise, if any other two population-host combinations are compared, it is found that there is great variability from year to year. All these clearly show that host plant preference of any given population is not fixed and that there is no fixed relationship between the responses of aphids to one host and their response to another. Combined analysis of variance done with the fecundity data from different years indicates that the years are significantly different ($P<.01$). It is clear from the data that various populations exhibit a great variation in their host plant preferences from year to year in a most unpredictable manner. Therefore, one year's attributes of aphid samples from populations can not be used to differentiate and recognize aphid populations in succeeding years.

Fecundity of aphids sampled from various populations on perennial hosts at variable intervals over the season in 1981 is presented in Figure 14. Analysis of variance shows (Table 17) that time intervals, response to different hosts and population versus host interaction are significant ($P<.01$). These illustrate that when the season progresses, responses of the populations to the hosts also change. This may presumably be through differential survival reproduction and/or dispersal. Similarly, there is no relationship between the responses of clones within any given population to one host plant and their responses to another host plant.

Figure 14. Fecundity of aphids sampled from different populations and when reared on different hosts in the field at variable intervals over the season (1981).

Analysis of variance was done on transformed $X^{.28}$ data.

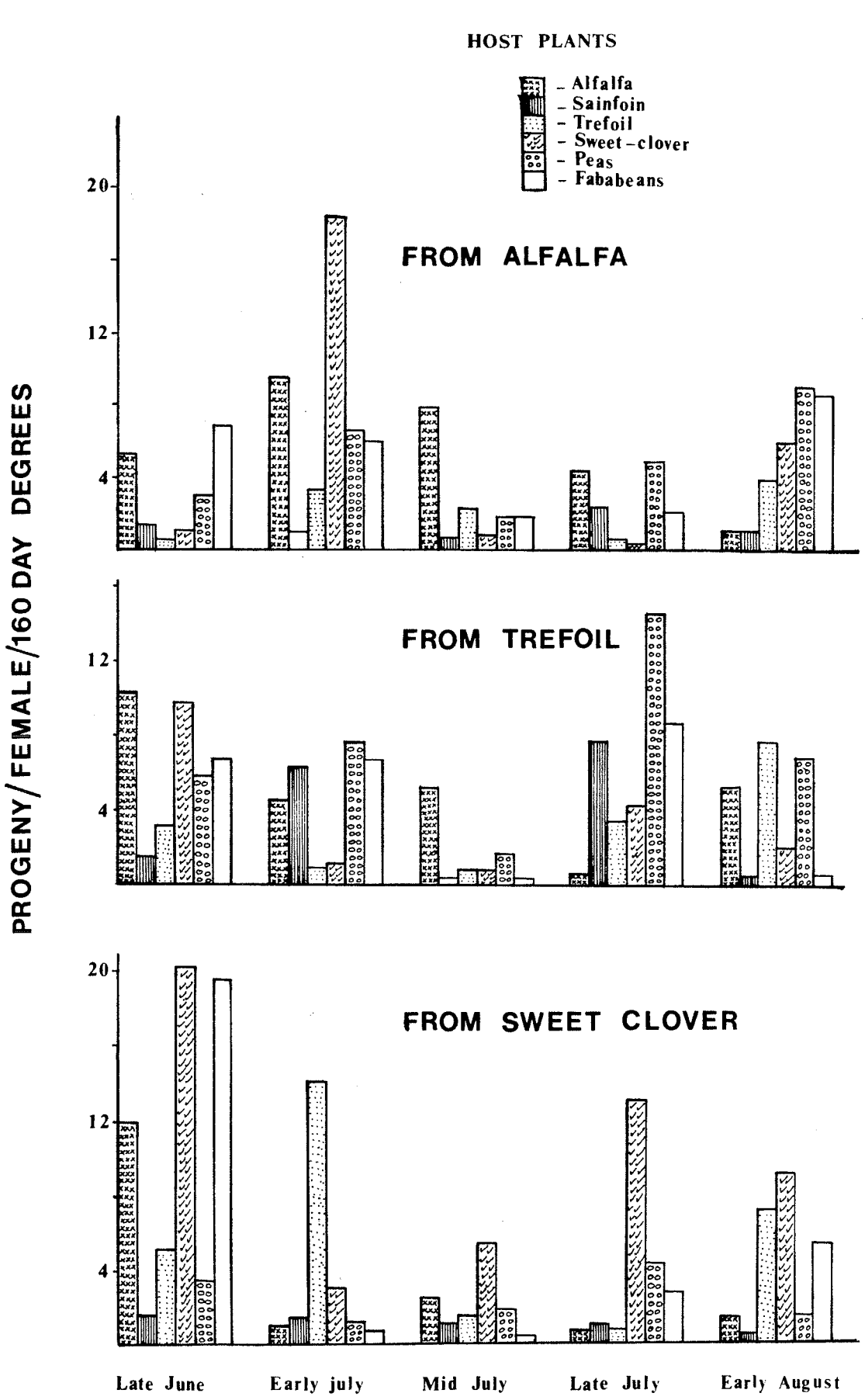

HOST PLANTS
- Alfalfa
- Sainfoin
- Trefoil
- Sweet-clover
- Peas
- Fababeans
PROGENY/FEMALE/160 DAY DEGREES
20
12
4
FROM ALFALFA
12
4
FROM TREFOIL
20
12
4
FROM SWEET CLOVER
Late June
Early july
Mid July
Late July
Early August

Table 17. Anova table for fecundity data of aphids sampled from alfalfa, trefoil, and sweet-clover tested on different hosts at variable intervals over the season in the field (1981)

Source of variation	Degrees of freedom	Sums of squares	Mean square	F - ratio
Time	4	4.82	1.20	2.59 **
Population	2	0.05	0.03	0.06 NS
Hosts	5	5.72	1.14	2.46 **
Time x population	8	5.71	0.71	1.54 NS
Time x hosts	20	15.98	0.80	1.72 *
Population x hosts	10	11.58	1.16	2.49 **
Time x population x hosts	40	20.64	0.52	1.11 NS
Replicates	3	0.86	0.29	0.61 NS
Error	267	124.19	0.47	
TOTAL		189.55		

Data transformation $Z: -X^{0.28}$

** Significant at 1% level.

* Significant at 5% level.

NS Not significant.

CHAPTER V

DISCUSSION

1. Introduction

The term biotype in insect biology has been used in the broad contexts of species, populations and individuals. It appears that there are two usages of which one is a general concept that applies to both individuals and populations of a species which share certain biological characteristics, with little or no knowledge of their genetic bases. The second concept is rather specific in which a particular gene for a certain characteristic of an insect is known to correspond with a particular gene in a host. For instance, virulence on the part of a pest and resistance on the part of a host and the genes responsible for that phenomenon.

2. Biotypic Phenomenon and Variability within Populations

In the case of the pea aphid, it is currently assumed, though seldom stated, that the biotypes are separable by clear-cut patterns of responses to certain plant species or varieties of a species (Auclair 1978; Cartier et al. 1965; Harrington 1945; Markkula and Roukka 1970a, 1971), without much knowledge of their genetic bases. In the present studies when the three 1980 clones which were collected from three different hosts, were tested they responded consistently and differently on different host plants (Table 4). These three clones might be assumed to belong to three different biotypes. When field populations on different hosts at the Research Station, Glenlea, were studied in 1981, they clearly

exhibited great variation within any given population, while populations were not significantly different in their responses to different host plants (Tables 6, 7, 8 and 9). Based on the performance of the three 1980 clones, if the sixty clones tested in 1981 are to be assigned to three different biotypes (Neiman 1971; Pathak and Painter 1959), some clones are found to share the characteristics of more than one biotype. Pathak and Painter (1959) tested various populations from distant locations by caging a known number of aphids on a particular host and then on the basis of fecundity, they assigned the populations to various biotypes. This method tends to mask any individual variation present within the aphid population. The extent of variation exhibited by various biotypes originating from diverse geographic locations (Auclair 1978; Cartier 1959, 1963; Cartier et al. 1965; Harrington 1945 in Chapter II, 4) was exhibited by different clones sampled from any particular population on any given host in both 1981 and 1982 studies. Therefore, it appears that field populations of the pea aphid are normally variable in biological characteristics as shown in the present studies. Under these circumstances, identifying and naming or otherwise labelling such biotypes (Cartier 1959; Harrington 1945; Neiman 1971; Pathak and Painter 1959) is necessarily arbitrary and could lead to confusion.

3. Seasonal Changes

The present studies have documented that the clones present on one particular plant species show some short term selection. This is expressed in terms of differential survival (Table 7), differential

fecundity (Tables 10 and 14) and differential alata production (Tables 11 and 15). This is followed by genetic recombination during sexual reproduction in the fall. There are no significant differences between populations in their biological characteristics in the spring. This is probably a selection process not unlike competition among different genotypes. Darwin (1859)* stated that competition was a primary force in natural selection, and he also stressed that competition or

> "the struggle will almost invariably be most severe between the individuals of the same species, for they frequent the same districts, require the same food, and are exposed to the same dangers".

Loaring and Hebert (1981) reported results of competition experiments on clones of Daphnia pulex Leydig in which they found that out of 12 experiments, in most cases only a single clone remained at the end of the study. Similarly, in studies on Asplanchina (Phylum:Aschelminthes), Snell (1979) observed the competitive replacement of one clone by another in as few as 5 generations. This occurrence of competitive exclusion might be expected as many experiments have shown, when two species compete for identical food in the same habitats, one species displaces the other in a few generations (Allan 1973; Neill 1975; Snell 1977). The number of clones may be high in the spring, but this variability is reduced in the course of the parthenogenetic generations presumably through differential survival, reproduction and/or migration. Consequently, a a majority of autumn individuals within a field may be much more

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*Darwin, C.R. 1859. The origin of species pp. 71 (1928 ed.), Dent., London, 488 pp.

homogenous in terms of their responses to different host plants. This is suggested in the present studies (Table 15) where twelve clones sampled from a population on alfalfa (var. Algonquin) late in the season in 1982 did not exhibit significant clonal variability with regard to their mean fecundity on all the four hosts tested ($P>.05$).

Aphids are known to be carried for hundreds of miles by prevailing winds (Johnson 1957; Medler and Smith 1960). As a result there is every possibility that late season sampling on any population might also include recent immigrants. This might add to the heterogeneity of the sample of clones in terms of their responses to different host plants. This fact and the short field season in Manitoba might be responsible for the difference still found among the clones sampled from most fields in the later part of the season in the present studies.

4. Annual Changes

The sexual generation in aphids represents the offspring of the parthenogenetic generations. The allele frequencies of the sexual generation represent the end result of selection, which has operated upon the parthenogenetic generations. The sexual phase of the aphid holocycle entails genetic recombination between genotypes. The resultant offspring in the following spring show some genetic variation among themselves which is accounted for by using such terms as biotypes, races, strains etc. Intra-specific variation may occur either within populations or groups of neighbouring populations, or between geographically separated groups of populations. Within a population, the range of

variation may be great or small, but it is subjected to environmentally induced selection pressures. As a result clonal variability is reduced (Table 15) in the course of parthenogenetic generations. Consequently, autumn individuals within populations are much more homogenous as compared to spring individuals. The present studies have shown that the biological variation among clones recognized represented the situation as it occurred in the year or time of the season when the clones were sampled and tested (Figures 11, 12, 13 and 14). These data show that there is no relationship between the responses of aphids to different host plants in one year and their responses to the same host plants in another year. Therefore, the attributes exhibited by clones cannot be used to separate and recognize similar clones in succeeding years. Frazer (1972) suggested that new biotypes of A. pisum arise annually by adaptation of parthenogenetic clones to different species of host plants. This indicates that the biotypes are annual phenomena.

One year's population increase of aphids is often different from the previous year's pattern (Figures 11 and 13). The reason may be that they are greatly affected by environmental conditions. It may be that early spring weather has many indirect effects, including the selection of some clones at the expense of others. The existence of such genetic variation within any given population may be one of the reasons why aphids can be so unpredictable with regard to their population growth.

5. Variability Between Populations

Field studies conducted over the three years did not show any differences among populations. Nor did laboratory studies conducted in 1981. However, laboratory studies conducted in 1982 with the samples of clones from two older alfalfa fields differed from each other with regard to their fecundity ($P<.05$) (Tables 12, 13 and 14). These two fields were different in several ways. Geographic separation of the fields might be responsible for the difference. Lamb and MacKay (1979) reported similar differences among natural populations of A. pisum located less than 23 km apart. This difference is based on migratory tendency (the number of alatae produced) of various populations. They also reported that fields that were very close had populations with similar migratory tendencies. Likewise, the alfalfa (var. Beaver) field sampled in 1982 and the alfalfa field sampled in 1981 were located close to one another at the Research Station, Glenlea. An analysis of variance carried out to compare the data from these two populations showed that the samples are not significantly different ($P<.01$). High selection pressures exerted by the application of insecticides every year on the aphid population on alfalfa (var. Algonquin) at Dugald, might be responsible for the virulent nature of those clones. The aphid populations at Glenlea were never treated with insecticides. However, variation among different clones between those populations was no greater than that of clones within populations ($P<.01$). This was true with regard to populations tested in 1981 as well.

The data are too limited to permit any firm conclusion on geographic relationships in biotypic phenomena. However, it is important to establish the relative status of intra-specific variation from widely different geographic areas, particularly where anholocycle prevails. In such areas, there is no genetic recombination possible. As shown by the present studies, selection and adaptation do occur among populations present on a particular host. Therefore, it is hypothesized that the populations of A. pisum in areas where anholocycle prevails would be relatively homogenous compared to those in areas where holocycle occurs. In tropical regions where anholocycle is said to occur, distinct agro-climatological areas prevail due to differential altitudes. In such areas diverse genotypes may occur that particularly adapted to local environments. In addition, the prevalence of a wide range of host plants can also contribute to divergences of genotypes. Since geographical populations are known to be concerned in the development of a species, it is thus important that studies should be undertaken on such geographically separated populations.

In apomictic parthenogenesis the effect of selection is opposed only by mutation. For instance, the corn-leaf aphid, R. maidis, appears to be entirely parthenogenetic in reproduction, males having been reported only a few times in the literature and eggs and egg-laying females not at all (Painter and Pathak 1960). Therefore, it appears that the only possible origin of biotypes in such cases would be through gene or

chromosomal alterations. Since the species concerned is parthenogenetic, the genes which cause these changes must almost certainly be dominant. In tropics where sexual reproduction in A. pisum is not reported to occur, biotypes could occur through gene or chromosomal alterations and also by immigration from other regions. Such mutations have occurred under observation in another aphid, Macrosiphum solanifolii (Ashm.) (Shull 1943). Apparently a similar start is responsible for the origin of the spotted alfalfa aphid biotype resistant to insecticides (Stern and Reynolds 1958).

The possibility of mutation leading to biotype formation could account for clonal responses to sainfoin in the present study. The high nymphal mortality and poor fecundity on some host plants particularly on sainfoin (Tables 8 and 9) cannot be accounted for by any possible parental effect because nymphs fed on other hosts in the same experiment showed normal survival and growth. However, it is assumed here that the maintenance of aphid cultures on fababeans had no drastic preconditioning effects which make sainfoin unpalatable. This high mortality may be caused by toxic or repellent substances in the foliage. Dethier et al. (1960) have suggested that some plants may contain substances which deter sustained feeding in addition to those having a toxic effect. Shaver (1974) suggested that high mortality can also be caused by metabolic inhibitors in plants or by insufficient quantities of specific nutrients required by the insect for growth. Out of a large number of clones tested in the present studies, only one clone was found to do well on sainfoin. This particular clone was among those that were sampled

during the later part of the 1981 season. It may be possible that this clone is a mutant which has a greater ability to feed on sainfoin than other clones tested.

Muller (1971) reported that it was possible to obtain hybrids between several biotypes of A. pisum including a viable hybrid between one green pea-attacking form and a red form which colonizes T. pratense as its principal host and cannot colonize peas. He also showed that inheritance of host plant selection is, in most cases, without dominance and F_1 hybrids of such combinations settled on the hosts of both parents. If no breeding barriers exist between biotypes and mating occurs at random, it is clear that the biotypes represent fairly simple genetic variants of one freely interbreeding biological species.

Most aphid species are host specific. This specificity must have lasted for long periods of time. Many common plant species seldom develop colonies on them although they are regularly attacked by common aphids. There are a number of reasons for the persistance of the resistance. Resistance to insect attack is part of the evolutionary strategy of plants, just as overcoming the protective mechanisms of plants is part of the evolution of phytophagous insects.

Theories of insect-plant co-evolution suggest that there should be genetic variation within insect populations in characters which control host selection and utilization (Feeny 1976). Oviposition (or larva-position by winged aphids) preference is one example of such a character, and genetic variation among individuals could cause differences among females in oviposition preference. Variation in oviposition preference

among the females in a population could have important evolutionary consequences. This type of variation would make a population more flexible, if the primary host(s) were not available. Some individuals might even prefer alternative hosts. Therefore, intra-population variation in host selection characters may play a key role in host shifts and insect plant co-evolution. Modes of speciation amongst parasitic insects including plant feeders centres on the suggestion that sympatric host race formation is relatively common in nature (Price 1980; White 1978). Some workers (Bush 1975a, 1975b) have suggested that some relatively specific insect herbivores may transfer occasionally to previously unsuitable host plants, and consequently such insects might develop barriers to mating with the parental population. But it is not certain whether such host races do occur in the field (Futuyma and Mayer 1980; Jaenike 1981). This area is one of considerable current discussion and criticism. Detailed field studies are most desirable to document whether such sympatric host plant associated biotypes do occur among the plant feeding insects.

Oviposition (larviposition) choice is especially important in insects which have immature stages that are relatively immobile. Hopkin's host selection principle (Hopkins 1917) states that a female's oviposition preference is biased in favour of the plant species she fed upon as a larva. The present studies indicate that the individuals collected from crop X did not prefer crop X more strongly than those collected from crop Y particularly during the early part of the season. The results show that the larviposition is not biased in favour of the host plant species they fed on as larvae.

6. Concept of Biotype and Agricultural Pests

The practical usage of the term biotype which was used to describe the responses of insect pests to different crops or cultivars of crops (Painter 1951) has recently been reviewed by Russell (1978) more widely in breeding plants for pest and disease resistance. Pathak (1975) listed seven species of insect pests including five species of aphids in which biotypes have been indentified. The remaining two species were the Hessian fly of wheat and the brown plant hopper of rice. The most significant biological characteristic of such biotypes is their ability to feed on crops resistant to some other biotypes. This association of virulence in a pest with resistance in a plant to that pest, is widely assumed to be characterized by a gene for gene relationship (Gallum and Khush 1980; Price 1980). However, such relationships are known in very few cases only, and none in case of A. pisum biotypes. In the brown plant hopper, three such biotypes with a known gene for resistance are said to occur (Pathak and Khush 1979). However, recent studies have documented great variation within each of the three biotypes of the brown plant hopper maintained at the International Rice Research Institute (IRRI), Philippines (Claridge and Den Hollander 1980; Sogawa 1981).

As it has been clearly shown in the present studies, biological variation in characteristics exhibited by different clones are not necessarily mutually exclusive. An individual or clone may belong to two or more biotypes (Tables 6, 7, 8, 9, 12, 13). Two clones that belong to one biotype with regard to their ability to feed on a pest resistant plant may belong to two different biotypes if another species of plant

or a variety of species is compared. Likewise, two clones belonging to the same biotype can differ on one and the same host or vice versa with regard to two different parameters estimated (Table 4 and 5).

As biotypes are temporally unstable, and often difficult to detect morphologically, the system of nomenclature currently being employed seems quite inappropriate for insects like A. pisum. As reported by Flor (1956), labelling of biotypes may be useful in the relationship between some fungal pests and their hosts. However, when biotypes such as those of A. pisum which have a wide range of variation and overlap widely with each other, the assigning of populations to particular biotypes is of very little value.

From the definition by Maxwell and Jennings (1980) quoted in Chapter II, it is clear that the concept of biotypes is used of both individuals and populations within one species of insect. However, the precise nature of this biological variation in A. pisum is not clear. Conflicting suggestions, based on little experimental evidence, have been made concerning the degree of genetic differentiation between them. But broadly based investigations on the morphology, cytology, biochemistry and behaviour of the clones in addition to genetic studies, are needed in order to understand the exact nature of these clones exhibiting diverse genetic variation which has led to the establishment of the concept of biotypes. However, until an efficient and reliable method of hatching of eggs of A. pisum in the laboratory is developed, studies on inheritance of resistance and other aspects of genetics appear rather difficult.

Present studies have elucidated to a great extent the exact biological significance of the variation among clones of A. pisum. Different authors have given various definitions to biotypes since the inception of that concept. Most of those definitions are misleading rather than enlightening, at least so far as the biological status of the insect is concerned. Among others, the definition given by Eastop (1973) has been widely used and referred to by various authors. According to Eastop (1973)*,

> "a biotype is a taxonomic concept mostly used by non-taxonomists, and it has been defined as consisting of all individuals of equal genotype. In aphids at least, equal genotype means behaving similarly as far as the researcher's immediate interests are concerned".

But the present studies have clearly indicated that when the researcher's immediate interests are broadened by involving a few host species or varieties of a species rather than limited to one or two host plants in the research, particular two or three biotypes which behave similarly on one host would no longer be similar on different hosts. Therefore, it appears that the sympatric biotypes of A. pisum prevailing in populations on any given host represent fairly simple genetic variants and the term biotype represents no distinct biological concept. However, the relative status of this intra-specific variation from widely different geographical areas, where anholocycle prevails, remains to be established.

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*Eastop, V.F. (1973). Biotypes of aphids, pp. 40 In 'Perspectives in Aphid Biology' Ed. by A.D. Lowe, Bull. No. 2, Ent. Soc., New Zealand 123 pp.

CHAPTER VI

SUMMARY AND CONCLUSIONS

The results of the experiments described above have important conclusions and ecological implications. Some of these will be pointed out below.

The three 1980 clones responded consistently and differently, suggesting that they belonged to three different biotypes. When field populations on different hosts were tested in 1981 they clearly exhibited tremendous variation within any given population. But the characteristics of populations were not significantly different. These populations were also found to include individuals with the characteristics of more than one biotype. In addition, different clones, from any population tested, exhibited variation among themselves to the same extent as is exhibited by biotypes having diverse geographic origin. Therefore, it appears that field populations of the pea aphid are normally variable in biological characteristics.

It was found that the clones present on a particular plant species show some short term selection during summer when reproduction is parthenogenetic. In the fall, as a result of genetic recombination during sexual reproduction, a different set of clones is generated and appears in the following spring. It was found that there is no relationship between responses of clones to different host plants in one year and their responses to the same host plants in another year. Therefore, it appears that the biotypes are annual phenomena. The number of clones may be high in the spring, but this variability is reduced in the course of partheno-

genetic generations, presumably through differential survival reproduction and/or migration. Consequently, autumn individuals within a population are more homogenous with regard to their responses to different host plants.

Samples of clones from the two populations tested in 1982 showed some differences. This may perhaps be due to the geographic difference, high selection pressures exerted by insecticides on one of the populations, or to the different varieties of the host, more than mere age of the population. These data are too limited to warrant any conclusions on geographic relationship. Relative status of this intra-specific variation of clones available from widely different geographic areas, particularly where anholocycle prevails, remains to be established.

Field studies indicate that the characteristics of the clones represent the situation in that particular year and should not be used to separate and recognize clones during succeeding years. Therefore, as suggested by Frazer (1972), in assaying plants for resistance to pea aphids, only fundatrices and their immediate offsprings which have not been subjected to selection should be used as test organisms. Moreover tests should be carried out over several seasons so as to expose varieties to all possible genotypes.

Clones exhibiting variable characteristics are not necessarily mutually exclusive. An individual or clone may belong to two or more biotypes. Therefore, the system of nomenclature currently being employed seems inappropriate as it tends to give a false impression of the biological significance of the pest by masking the inherent variability of

the pea aphid populations.

Absence of an efficient method of hatching A. pisum eggs in the laboratory has become an obstacle in the progress of further work on genetics of variable clones. Broadly based investigations on the morphology, cytology, biochemistry and behaviour of the clones in addition to genetic studies will elucidate the exact nature of this biological variation in A. pisum.

Definitions given by various authors to biotypes seem inadequate and misleading with regard to the biological significance of biotypes. It may be concluded that the sympatric biotypes of A. pisum prevailing in populations on any given host represent fairly simple genetic variants. Therefore, it is suggested that the practice of identifying and numbering of clones of A. pisum should not be continued as it may give a false impression of the biological status of the pest.

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Appendix 1. The meterological data during the period of field studies (The Research Station, Glenlea, Manitoba)

I. Temperature (^{o}C) monthly mean

	May	June	July	August
1980	15.0	16.5	19.5	16.0
1981	12.0	16.2	19.5	19.9
1982	13.1	13.4	19.5	16.8

II. Rain fall monthly total (mm)

1980	45.5	64.2	21.8	117.7
1981	26.0	88.7	58.8	90.0
1982	23.9	64.1	83.6	30.5

III. Relative humidity (%) monthly mean

1980	96.6	76.5	59.5	-
1981	67.2	84.1	84.8	88.8

IV. Monthly mean for the crop season (May-August)

	1980	1981	1982
Temperature (^{o}C)	16.75	16.90	15.70
Rain fall (mm)	62.30	65.88	50.53
Relative humidity (%)	77.53	81.23	-

Appendix 2. Hydroponic Solution:contents

	Stock solution gm/ℓ	Nutrient solution mℓ/ℓ
KNO_3	101.11	2
KH_2PO_4	136.09	2
$Cu(NO_3)_2.4H_2O$	236.16	3
$MgSO_4.7H_2O$	246.50	2
FeEDTA*	36.71	1
Micro elements		
H_3BO_3	2.50	
$MnCl_2.4H_2O$	1.50	
$ZnCl_2$	0.10	1**
$CuCl_2.2H_2O$	0.05	
MoO_3	0.05	

*Ethylenediaminetetra - acetic acid $\left[CH_2.N(CH_2.COO)_2\right]_2$ FeNa (Ferric monosodium salt).

**1 ml of a stock solution containing all the micro nutrients is used.