STUDIES ON THE ECOLOGY OF CINARA TODOCOLA Inouye (HOMOPTERA:APHIDIDAE) WITH SPECIAL REFERENCE TO THE DISPERSAL OF WINGLESS APHIDS

（トドマツオオアブラムシの無翅虫の分散に関する生態学的研究）

BY

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SUMMARY

Cinara todocola is a well known pest of Sakhalin-fir (Abies sachalinensis) trees in Hokkaido, Japan. It attacks trees less than 10 years old, and the percentage of infested trees often increase when no winged females exist, indicating that dispersal is done by wingless aphids.

The effects of plant spacing, interplanting with non-host plants, shade and direct sunlight on dispersal of C.todocola and their application in forest management was studied. Increased plant spacing, interplanting with non-host plants and direct sunlight prevented/delayed aphid dispersal. However, plant mortality was high since many aphids concentrated on just a few trees.

At first each aphid occupied its most suitable position on a plant, and reproduced there. When it become overcrowded some moved to other positions. Such movement occurred suddenly rather than gradually when the population density exceeded a certain level (over 300 individuals per 55cm mean height sapling) under controlled and in open area conditions. This movement, which involved adults and young insects, lead me to speculate that there must be a threshold for mass movement. It is also very difficult to estimate at what colony size aphids begin to disperse, since movement was observed even on a small colony of four. Young aphids tended to stay with their mother, but later they began to move, especially when they reached the 3rd instar stage.

Overcrowding, host plant conditions, presence of natural enemies and brushing by dispersing aphids influenced aphid dispersal. Overcrowding of population was avoided by intra- and inter tree movement. Temperature influenced dispersal starting time and was earlier at high than low temperatures. During dispersal, when emigrating aphids reached ground level, most turned back and climbed the tree again.

C.todocola has a high walking ability compared to tall tree, herbaceous, and agricultural aphid species. The 3rd instar larvae walked longer distance than other stages. It is thus suggested that one of the important functions of this instar is dispersal since no winged female aphids were produced. The 4th instar larvae could not walk long distances because it is thought that, when it reaches this stage it has already started to invest in reproduction and so it will also be too costly for the clones to invest in both dispersal and reproduction at the same stage. Although the proportion of the dispersal investment to body weight was not calculated , it is thought that the ratio is higher in the 3rd instar larvae than other stages. The longer walking distance shown by stem mothers could be due to their lager body size.

Higher population growth was observed in June/July and September/October which is related to good food quality in spring and autumn. However, aphids born in the first generation were larger and heavier than those born in later generations. Aphid population growth was characterized by : Clumped spatial distribution within some plots, steep and steady population growth, and violent fluctuations in population density. These characteristics may have resulted from combinations of physiological traits intrinsic to the insect and the environment. Population peaks were usually followed by dispersal. Ant attended colonies had higher population growth rates compared to unattended ones.

In 1993 and 1994 proportion of trees with aphids attended by ants was 96% and 80%, respectively. As a result, aphid spread was low in 1993 since ant nests restricted their dispersal and encouraged high population growth by protecting them from natural enemies. This lead to the death of 64% of trees infested with aphids in 1993 compared to 42% in 1994.

Maximum dispersal distance observed in the field was 16m. Aphids moves randomly, and their walking distance changes with time. When an object is placed in front of an aphid most tended to be a little directional, and they were most attracted to green, followed by yellow colours. They were also attracted to larger rather than smaller objects.

It is recommended that a wider plant spacing interplanted with non-host plant species be used to reduce chances of aphid infestation in Sakhalin-fir plantation forest.

論文の内容の要旨

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論文題目　Studies on the ecology of *Cinara todocola* Inouye (Homoptera: Aphididae) with special reference to the dispersal of wingless aphids
（トドマツオオアブラムシの無翅虫の分散に関する生態学的研究）

*Cinara todocola*は日本の北海道でトドマツの害虫としてよく知られていて、10年以内の造林地に発生する。分散は通常は有翅虫によって行われる。しかし、有翅虫がいなくても寄生されている木の割合がしばしば増加する。このことは、造林地内の分散は無翅のアブラムシによって行われることを示している。

苗木の間隔、寄生の対象とならない木の存在、直射日光などが*C. todocola*の分散に与える効果を解析し、アブラムシの発生しにくい森林管理のあり方を研究した。苗木の植裁間隔の増大、非寄生木の存在、直射日光はアブラムシの分散を阻害したり遅延させたりした。

最初それぞれのアブラムシは一本の木において最も適当な場所に生息し繁殖した。密度が高くなると、アブラムシは他の場所へ移動した。このような移動は個体群密度が、実験室内と野外共に、平均樹高55ｃｍで約３００頭の時に起こった。この移動には成虫と幼虫がふくまれていた。多数の個体が移動を開始する閾値の密度が存在するに違いないと思われる。しかし、コロニーについては、4個体の小さなコロニーでも移動は観察されるので、

どの大きさのコロニーが分散を始めるかを予想することは非常に難しい。高密度な状態と寄主植物の状態、天敵の存在、アブラムシ同士の接触はアブラムシの分散に影響する。樹内と樹間を移動することによって過密の程度は下げられる。

*C. todocola*は高木性，草木性、農業害虫としてのアブラムシなどの種と比べて高い歩行能力を持つ。3齢幼虫は他の齢級のものよりも長い距離を歩く。この齢の重要な機能の一つは分散であると考えた。体重に対する分散の投資の割合を計算できなかったが、その割合は他の齢より３齢幼虫において高いと思われる。幹母に見られる長い歩行距離は体の大きさに依存したものであると思われる。

高い個体群の成長は6月／７月と9月／１０月で観察された、春と秋に食べ物の質が良かったからであると思われる。しかし、第１世代のアブラムシは次の世代のアブラムシより大きく重かった。アブラムシの個体群動態は次のような特徴を持っている、すなわち集中分布、急速な個体数の増加、個体群密度の激しい変動などである。これらの特徴は昆虫と環境に内在する生理学的特徴が合わさったものから生じたかもしれない。個体数がピークに達すると分散が続く。アリが共生しているコロニーでは共生していないコロニーよりも高い個体数成長を示した。

1993年と１９９４年の、アリとアブラムシが共生している木の割合はそれぞれ９６％と８０％であった。アブラムシの分散は1993年は低かったが、アブラムシの分散を制限し、天敵から守ることによって高い個体数成長をうながしたと考えられる。このことにより１９９３年の木の６４％はアブラムシの寄生を受けて枯れた。1994年は４２％であった。

野外で観察された最大分散距離は１６ｍだった。アブラムシはランダムに移動し、それらの歩行距離は時間と共に変わる。なにかの物体がアブラムシの前に置かれるとほとんどの個体はその方へ動く。色については緑色に最もひかれ、次は黄色であった。小さな物よりむしろ大きな物にひかれた。

以上のことから、苗木の植え方を工夫することによって　トドマツオオアブラムシの発生を制御することが可能であると結論された。

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1.0 CHAPTER 1

INTRODUCTION

Cinara species is one of the most serious groups of insect pests of coniferous trees, both in the temperate zone and in the tropics. It is not yet known if these insects are vectors of any disease causing agent. It has been reported that considerable yield losses can occur due to their feeding activities. Cinara spp. are considered as one of the most destructive insects in young Sakhalin-fir (Abies sachalinensis) plantations in Hokkaido, Japan (Yamaguchi,1976).

Because of their economic importance, numerous studies have been done especially on the temperate species, Cinara todocola, (Furuta,1976; Yamaguchi,1976; Yamaguchi and Takai,1966; Furuta and Aloo, 1994). Odera (1990) reported that the spread of Cinara cupresii in southern and central Africa and its fast advancement into Tanzania and Uganda has been received in Kenya with great apprehension.

There are very few studies on the dispersal of wingless aphids compared with winged ones . Most entomologists consider that winged aphids play an important role in the dispersal process, neglecting the role of the wingless ones (van Emden, 1972). This is because in agricultural crops or annual plants, dispersal of winged aphids is more important. Cinara todocola, however, attacks young trees less than 10 years old and the percentage of infested trees often increases in seasons when no winged females exist. Which means that within a plantation the wingless aphids disperse and make colonies (Furuta, 1976). Therefore, dispersal of wingless females seems to be an important factor in the spread of the aphids within a plantation. In forestry, dispersal of wingless aphids between and within trees is of great importance since they attack young trees. These insects are sometimes found walking on the ground around the host plants. It infests only the branches, stems and sometimes roots of Sakhalin-fir saplings below 2m in height which are less than 10 years old. For some 3 to 4 years after planting the aphids feed on almost all parts of the stem and branches of the tree. Thereafter, their feeding places are gradually restricted to the upper part of the stem or branches as the tree grows (Yamaguchi,1976). Both nymphs and adults of C.todocola suck sap from the phloem of the Sakhalin-fir, causing severe damage called "Aphid burn".

Yamaguchi (1976) conducted extensive studies on the population dynamics and polymorphism of this aphid, but unfortunately dispersal by walking was not studied, although this insect may have developed walking adaptation features compared to other aphids. Furuta and Aloo (1994) failed to recommend an optimum spacing distance that will reduce incidence of aphid attack, although a biological method for control of this aphid was proposed. In Cinara bogdanowi (Furuta and Takai,1983) the movement of wingless aphids is limited, which only allows slight inter-tree dispersal within a plantation, and only dispersal of winged adults allows the aphids to reach other trees.

Although most aphid species dispersal is by winged forms, Cinara todocola is undoubtedly the best example of this rare case. This could be due to the distribution and physiological conditions of its host that allow it to behave like this, due to the following facts:(1) This aphid stays on branches, stems or roots of young trees and has good access to land (like herb aphid species). (2) Host trees distribute widely in both natural forests and young plantations, and wingless aphids have a high possibility to find a new host. (3) In natural forests where young trees are regenerating, usually there are few herbs or grasses which disturb the walking of this aphid. (4) Once an aphid succeeds in finding a new host, its descendants can stay there for at least several months and often for several years. Although aphid-host relationship on herbs may fulfill two or three of these 4 conditions, only aphids on young woody plants fulfill all of them. Therefore, wingless aphids must play an important role in the dispersal of some woody aphids like Cinara todocola. It can be hypothesized that Cinara todocola has some morphological and physiological adaptations for walking.

It is said that dispersal can play an important role in the persistence of animals populations living in unstable, heterogeneous habitats (Reddingius & den Boers,1970; Roff, 1974a, 1974b; May,1974; Levin,1976). It has been demonstrated that dispersal acts as a stabilizing factor (Roff,1974a) which brings about the "spreading of risk " in den Boer's (1968) sense. Kuno (1981) has demonstrated theoretically that in a heterogeneous habitat, the dispersal of individuals, even when it is random and density dependent, may have a pronounced effect of raising the average reproductive rate of the whole population. This implies that in such a population the habitat instability has been converted by dispersal into condition profitable for the population. It has been said that alatae production and dispersal has been regarded as means of regulating numbers, and in several species it is most marked when there are large populations. However, the production of alatae at a particular time of the year, even when the aphids are reared individually reveal that the primary role is dispersal (van Emden,1972).

To establish an efficient strategy to control C.todocola, the basic population characteristics of the species in the regions concerned must first be understood on the basis of field population data. In particular, analysis of distribution pattern is an essential first step for better understanding of its population dynamics. Yamaguchi and Takai (1977) reported that the impact of aphid attack on newly planted trees is severe and lessens as trees grow, therefore, the time of initial invasion and spread of aphids within a plantation is very important. Understanding of the dispersal distance of C.todocola is important for prediction of outbreaks and for determination of the range of direct control by the use of synthetic sex pheromone, chemical or silvicultural methods.

This study investigated the effects of different treatments, i.e. plant spacing, inter-planting with a non-host plant, and shade and light on the dispersal of Cinara todocola and their application in forest management. Concurrently, to support this experiment, laboratory experiments in a controlled chamber and field experiments were carried out on the population dynamics of this aphid. A walking experiment and aphid response to object sizes and different colours were also conducted. Comparison of walking ability of this aphid with other species of aphids,and daily dispersal pattern was also done.

1.1 BIOLOGY AND LIFE HISTORY

Aphids are small, soft bodied, plant sucking insects, several or all generations comprise parthenogenetic females which do not require fertilization and are viviparous. The life histories of the members of Cinara group are very similar. They occur in the coniferous spending their entire life on their preferred host, not migrating to others, as do many species belonging to other groups. The winter is passed in the egg stage. The first few generations in the spring are apterous, viviparous females, later winged females occur and finally winged or wingless males and oviparous females. Aphid morphs differ in both their behaviour and structure. In few a species there can be as many as 8 morphs that differ at least in their external morphology. Polymorphism is characteristic of aphids. Aphids anticipate the seasonal changes in habitat quality by producing a sequence of morphs that are each adapted to the conditions they are likely to experience.

Cinara todocola is a holocyclic and monoecious species. Eggs hatch in April or in early May to give apterous, viviparous parthenogenetically reproducing fundatrices (1st generation). Part of the offspring produced, develop into alate virginoparae which emerge and disperse from late June to mid

July (Yamaguchi, 1976). Consequently, the number of trees attacked increase markedly during this period. Winged females also appear in the 2nd generation but the proportion is quite small. In the subsequent parthenogenetic generations almost no alatae are found in the field. In September apterous oviparous and alate males are produced, which mate and the oviparae lay over-wintering eggs on needles from mid- October to mid-November. Cyclical parthenogenesis occurred in which sexual generation followed after generations of asexual reproductions. The production of sexual morphs is triggered by environmental cues and usually has an annual periodicity (Dixon 1985). Parthenogenesis is widely spread in plants but in animals is commonly found only in rotifers, cladocera, cynipids and aphids (Maynard Smith,1984).

There are 3 nymphal instars in the apterae, including fundatrices and four in alatae. Nymphal development of the alatae takes 5 days longer than that of apterae (at 15 ℃). The fecundity of the fundatrices is very large. The average number of the offspring produced is approximately 103 compared with 46 in the other apterae and 35 in alates at 15℃ (Yamaguchi, 1976). Temperatures influence fecundity as well as the rate of development (Campbell and Mackauer,1977). The fundatrices are relatively sessile while the apterous virginoparae of the later generations are more agile. Although the nymphs of the immature stage usually gather around their mothers and do not move, the third instar nymphs and teneral adults often leave the aggregate which they have formed. Appendix 1 shows the life history and different morphs of C.todocola.

The high rate of increase of populations is due to telescoping generations and parthenogenesis, occurrence of different forms or morphs, and is one of the characteristics of this aphid. Cinara todocola belongs to the insect superfamily Aphidoidea, within the order Homoptera, the plant sucking bugs. Primeval aphids were probably polyphagous and fed on the parenchymatous and phloem tissues of plants, and monophagy is a recent development in aphid evolution (Heie, 1967). Aphid small body size may be caused as a result of a parasitic way of life. About 80% of the subfamily Lachninae in which Cinara belongs live on conifers and are generally regarded as primitive (Heie,1967). Although Heie (1967) regarded Lachninae as primitive, whether this is true or wether it is one of the most advanced groups of aphids is a major issue on which there is no agreement (Dixon,1985).

Although aphids have a world-wide distribution there are fewer species in the tropics than in temperate regions. This could be due to the harsh environment of the tropics and subtropics and it is difficult to understand why aphids have not flourished as a group on the rich tropical and subtropical floras (East top, 1973). Dixon (1985) reported that in the tropics and subtropics where floral diversity is very high, few species of plants are apparent, enough to sustain an aphid species and due to this. Holmann (1971) reported that proportionately more aphids are polyphagous in the tropics than in the temperate regions. The greater number of aphids in the temperate regions can be due to the fact that in temperate regions there are fewer plant species than in the tropics and the commonest ones are, apparently enough to sustain one or more species of aphids. This is combined with the greater niche diversity produced by seasonal changes in habitat quality in temperate regions.

There is a big difference in the quality of the food available to aphids feeding on trees and herbaceous plants. Aphids assimilate more energy and achieve more growth per unit of sap when feeding on herbaceous plants than they do when so on trees (Dixon, 1975; Llewelyn, 1982), due to lower amino-nitrogen content of the phloem sap of trees (Dixon, 1975). Generally, the more structurally complex plants like trees are regularly infested by more species of aphids than herbaceous plants, although in grasses two species of aphids may co-exist. Increase in structural complexity that results from increase in the size of an individual plant can sometime results in the loss of species. Cinara todocola tends to infest young Sakhalin-fir and is rarely found on plants more than 14 years old. This is thought to be because the aphids feed at the tips of branches and so, on older trees they are more exposed to extremes of temperature and less well protected from their natural enemies by ants. Thus in addition to having more species of aphids overall, trees are likely to both gain and lose species as they increase in size and structural complexity (Yamaguchi, 1976).

Aphids that feed on the woody parts of the plants are often larger than those that feed on leaves, because of the depth of the phloem elements. Aphids species feeding on herbaceous or annual plants are very much affected by weather. Changes in weather result in changes in the relative abundance of herbaceous plants from year to year, and from place to place within a community (Grubb et al., 1982). The relative abundance of trees is less likely to be affected by year to year changes in weather. Therefore, aphids living on herbaceous plants are likely to experience years in which their host plants are rare or of poor quality or both. In such years the specific aphids associated with the plants will decline in numbers, and are likely to take sometime to recover when their host plants become more abundant again. Aphids living on trees, although affected by changes in weather nevertheless tend to be relatively abundant, at least for part of the year.

In communities of herbaceous plants, change in the relative abundance of the species from year to year possibly prevent some monophagous species of aphids from fully exploiting their host plants every year. Polyphagy is confined to a few species belonging to one subfamily, the Aphidinae but, what is possibly more important, it is confined to aphids living on herbaceous plants.

Irrespective of whether they live on herbaceous plants or on trees, aphids are opportunists exploiting ephemeral habitats which are continually being created (Dixon, 1985), increasing in numbers when conditions are more favourable. Number of individual species can, and often do, become very numerous within a short period of time.

2.0 CHAPTER 2

FIELD DISPERSAL AND POPULATION DYNAMICS

2.1 Objective

To study the effects of plant spacing, shade and interplanting with non-host trees on the dispersal and population dynamics of Cinara todocola.

2.2 Study site

The experiments were carried out over 2 years (1993-1994) in the Tokyo University Forest Experimental station in Tanashi, 23 km from the Tokyo University. The station is about 9.01ha. in area 60m above sea level and is located on flat land. The upper black soil layer is about 50cm deep and below it is a red soil. Annual mean temperature is about 13.7℃ and annual mean rainfall is about 1,400mm. It is bounded by the University farm, houses and an atomic research station.

Abies sachalinensis saplings are the natural host for C.todocola in Hokkaido and were brought to Tanashi and planted in 8 plots at different spacings. Some plots were interplanted with Pinus thunbergii (black pine), a non-host plant. Table 1 shows the treatments used in this experiment. All plots were surrounded by trees:

Table 1. Treatments used in spacing experiment.

Plot No	Plant spacing (m)	No.host plant	Plot size m2	Plot condition shade/open	Interplanted with black pine
1	2x2	35	96	shade	no
2	4x4	25	144	shade	yes
3	2x2	35	96	open area	no
4	8x8	24	560	open area	yes
5	4x4	25	256	open area	no
6	4x4	25	144	shade	yes
7	8x8	21	480	shade	yes
8	4x4	25	256	shade	no

Plot 1.

This plot was under the shade of broad leaf trees (area approx. $96m^2$) and 35 saplings were planted at a spacing of 2X2m. On one side of the plot there was a foot /path and the rest of the plot was surrounded by broad leaf trees.

Plot 2.

This plot had 35 trees planted at a distance of 4X4m under an old conifer stand of red (Pinus densiflora) and black (Pinus thunbergii) pines. Black pines were planted between the host plants to study the effects of interplanting on the dispersal of C.todocola. The plot size was $144m^2$, surrounded by conifer trees.

Plot 3.

This plot had 35 trees planted at 2X2m spacing in an open area in Nursery 2. On one side of the Nursery there was a road and the rest of the area was surrounded by trees. Plot area was about $96m^2$.

Plot 4.

This plot consisted of 24 trees in an open area planted at 8X8m spacing, in Nursery 2 and interplanted with black pine. Plot size was about $384m^2$.

Plot 5.

The plot had 25 trees planted at 4X4m spacing in an open area in Nursery 3, with a total area of $256m^2$. On one side of the nursery there was a road and the rest was surrounded by trees.

Plot 6.

Twenty five trees were planted under an unclosed canopy of young red pine trees in Nursery 3 at a plant spacing of 4X4m and interplanted with black pine. Plot size was about 144 m^2.

Plot 7

Twenty one trees were planted under an old mixed pine stand (black and red pine) at a distance of 4X4m apart, interplanted with black pine. Plot area was about $480m^2$. Due to pine wilt nematode attack most of the red pine trees were felled . This caused light to penetrate into the plot.

Plot 8.

Under the same pine stand as used above, 25 trees were planted at 4X4 spacing. Plot size was $256m^2$.

2.3 Inoculation of aphids

Aphids were first inoculated onto 15 host plants of Abies sachalinensis before planting into the field in April. To protect aphids from predation, saplings were covered with vinyl cloth. In May, the plant at the center of each plot was replaced by a tree infested with 100 aphids. This experiment was conducted over a 2 year period. In the second year it was made sure that no aphids were on the planted trees by removing all the eggs laid in the previous year.

2.4 Data collection

The following information was collected once per week:

- Dispersal of aphids to adjacent trees (numbers and time).
- Number of aphids on the central plant and on adjacent trees.
- Number of colonies per tree and number of aphids per colony.
- Presence of predators or parasites.
- Climatic conditions.

2.5 RESULTS.

2.5.1 Dispersal

Initial dispersal rate was higher in plots that were planted at closer spacings and in those under shade (Table 2).

Table 2. Dispersal of C. todocola to adjacent trees one month after planting from the center tree in 1993 and 1994

1993

Plot No.	Initial No. of aphids	Tree No. (*)centertree	Distance from centertree(m)	Number of aphids	Date of observation
1	(9) 100	18*		280	23.Jun
		19	2	15	23.Jun
2	(5) 100	13*		130	30.Jun
		12	4	10	30.Jun
3	(2) 100	18*		100	22.Sep
		17	2	3	22.Sep
4	(2) 100	10*		530	29.Sep
		15	4	10	29.Sep
8	(7) 100	13*		130	1.Jun
		8	12.65	6	1.Jun
		9	5.66	20	1.Jun
		11	16	10	1.Jun
		1994			
1	(14) 100	18*		11	1.Jun
		6	5.66	28	1.Jun
		11	4.47	45	1.Jun
		12	2.83	5	1.Jun
		16	4	45	1.Jun
		17	2	16	1.Jun
		22	2.83	80	1.Jun
		27	4.47	2	1.Jun
		28	4	45	1.Jun
		29	4.47	120	1.Jun
2	(11) 100	13*		75	1.Jun
		3	6.32	45	1.Jun
		6	4	15	1.Jun
		7	5.66	35	1.Jun
		10	2.83	10	1.Jun
		12	4	1	1.Jun
		14	4	10	1.Jun
		16	2.83	10	1.Jun
3	(3 100	18*		180	1.Jun
		1	7.2	36	1.Jun
		22	6	75	1.Jun
4	(2) 100	10*		280	1.Jun
		12	16	230	1.Jun
5	(3) 100	13*		150	1.Jun
		16	8.25	15	1.Jun
		18	4	130	1.Jun
6	(5) 100	13*		56	1.Jun
		10	5.66	2	1.Jun
		12	4	6	1.Jun
		24	6.32	20	1.Jun
7	(10) 100	0*		120	1.Jun
		17	10	6	1.Jun
8	(7) 100	13*		50	1.Jun
		7	5.66	10	1.Jun
		12	4	15	1.Jun

( )=Total number of trees with aphids by the end of the expt.

It was difficult to monitor subsequent dispersal rate after the aphids have moved to more than 2 trees because of inter-tree movement. To solve this and to see at what colony size aphids started to move, experiment 2 was done. In 1993 aphids in plots 5 (4X4m- open area), 6 (4X4m-shade+non-host) and 7 (8X8m-shade+non-host plant) did not disperse at all from the center tree one month after planting. This could have been due to direct sunlight, wider spacing or the presence of non-host plant between the host plants. These conditions probably reduce the chances of locating a host and also survivorship. The effect of shade is clearly seen in plots 1 (2X2m- shade) and 3 (2X2m -open area). In plot 1, aphids were first observed dispersing on June 23 and in plot 3 on September 22. The effect of interplanting was seen in plots 2 (4X4m-shade+non-host) and 8 (4X4m-shade) as aphids first dispersed in plot 8 on June 1 and on June 30 in plot 2. Interplanting with non-host plants not only delayed dispersal but also decreased the number of trees infested in a plot. However, the population growth of aphids per tree was very high, and this resulted in the death of host plants as observed in figure a.

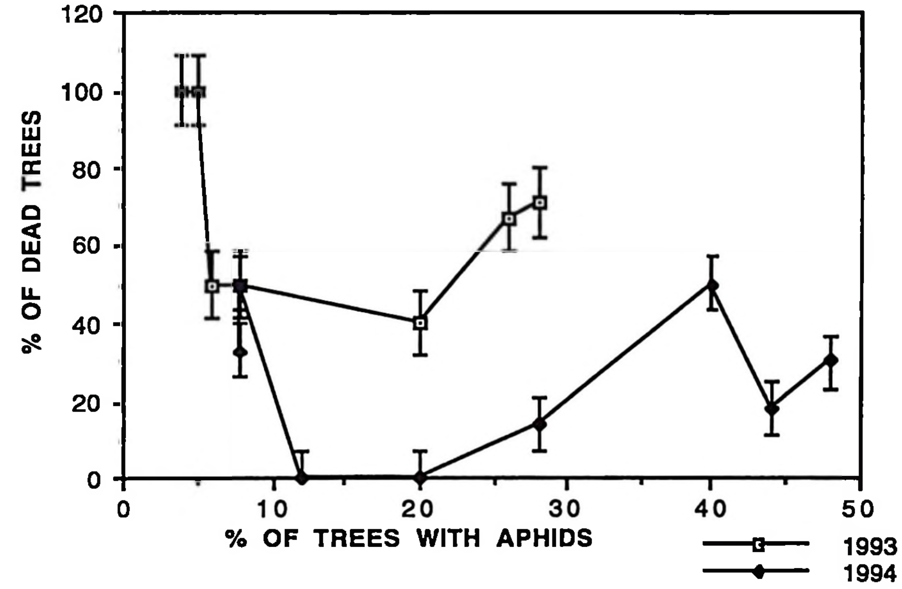


Figure a Percentage of trees with aphids to the percentage of dead trees in 1993 and 1994.

Immediately after the aphids had established ants were found attending them. There were 3 species of ants associated with C.todocola. Table 3 shows species of ants associated with this aphid. Not all trees with aphids were attended by ants but population size of those colonies attended by ants were growing faster. Table 4 shows the relationship between the number of trees with aphids to the number attended by ants. In 1993 the proportion of trees attended by ants was 96% (n=28) and in 1994 was 80% (n=44). Ants were sometimes found to carry aphids down along the stem to the root zone, but it was not clear if they were trying to protect the aphids or otherwise. By constructing earth tunnels around aphid colonies, ants restricted aphid movement. This resulted in high aphid population growth which damaged host plants. It was found that as host plant health deteriorated, the number of ants attending aphids also decreased and aphids started to disperse to nearby trees.

Table 3. Species of ants associated with C.todocola.

Plot No.	Species of ants	Japanese name
1	Lasius hayashi Yamaguchi & Hayashi	Hayashi - ke ari
2	Lasius hayashi Yamaguchi & Hayashi	Hayashi - ke ari
3	Camponotus japonicus Mayr	Kuro Ooari
4	Pristomyrmex punges Mayr	Amime ari
5	Camponotus japonicus Mayr	Kuro Ooari
6	Lasius hayashi Yamaguchi & Hayashi	Hayashi - ke ari
7	Lasius hayashi Yamaguchi & Hayashi	Hayashi - ke ari
8	Lasius hayashi Yamaguchi & Hayashi	Hayashi - ke ari

Table 4. Relationship between number of trees with aphids to number attended by ants in 1993 and in 1994.

Plot No.	No.of trees per plot	Trees with aphids 1993	1994	Trees with ants 1993	1994
1	35	9	14	9	14
2	25	5	11	5	8
3	35	2	3	2	3
4	24	2	2	2	2
5	25	1	3	1	2
6	25	1	5	1	3
7	21	1	10	1	8
8	25	7	7	6	4

Table 5. Relationship between number of trees with aphids to dead trees in 1993 and 1994.

Plot No.	No. of trees per plot	% of trees with aphids 1993	1994	% of dead trees 1993	1994
1	35	26	40	67	50
2	25	20	44	40	18
3	35	6	8	50	33
4	24	8	8	50	50
5	25	4	12	100	0
6	25	4	20	100	0
7	21	5	48	100	30
8	25	28	28	71	14

Percentage of dead trees in 1993 was higher than in 1994 as shown in table 5. This could be due to the fact that aphids did not disperse from the center plants. Some aphids were observed to move downwards along the stem and when reaching the stem base most turned back and climbed again, probably after assessing the risk of dispersal which might have been higher than staying on a deteriorated host plant. The summer of 1994 was very hot, temperatures reaching 37°C, and most aphids were found to be restless, and the movement was very conspicuous, shifting from the terminal shoots and setting along the stems in those plots which were under direct sunlight. Wind did not have any significant influence on aphid dispersal since all the plots were surrounded by trees. However, rainfall was found to have a significant effects on the aphid population, during rainy days aphids abandoned terminal shoots and settled along the stem and some were knocked/washed away by rain drops. Ant nests not only protected aphids from being washed away and restricted their dispersal but also encouraged high population growth by protecting them from natural enemies. However, observations showed that aphids were easily preyed upon by hunting spiders when they were lost or tried to escape from the colony.

Spiders were the most common predators followed by Coccinellid and syrphid larvae. Wasps were found flying around but it was not clear if they were parasitizing aphids. One tree in 1993 and 2 trees in 1994 had syrphid larvae, and all aphids abandoned those trees. To study the presence of predators/parasites, ten pit-fall traps were set per plot, and table 6 shows the composition and the number of different species of living organisms found in each plot. Pit-fall traps did not show many aphid predators/parasites. Spiders were the only aphid predator found in the pit fall traps.

Aphids were first found at the top of the plant, and as the population increased they moved downwards on the side branches and the stem. Some walked along the stem and when reaching the ground some continued to move, but most turned back and started to climb the tree again. Thus aphids seemed to prefer young plant parts. When the population density was low they were found on young shoots at the top of the plant and as crowding started they moved and settled along the branches and stem. Sometimes this movement continued into adjacent plants.

Apterous oviparae in the mature nymphal and adult stages tend to keep away from each other and disperse to the terminal twigs of the tree where they deposit their eggs. This dispersion sometimes extends to the surrounding trees, especially under high population densities. During initial dispersal, the maximum distance traveled by aphids was 16m in 1993 and 1994 (table 2). This distance was measured as a straight line from the center tree, however actual distance may be more than this since aphids do not walk in a straight line and locating a host is a random process. Although in plot 1 (1993) the number of aphids on the center tree was higher than in plot 8, dispersal rate in plot 8 was faster and more trees were infested than in plot 1. This was thought to be due to the late establishment of ants in plot 8 which allowed free movement of aphids. In plot 1, aphids were restricted by the ant's earth tunnels. Although ant tunnels were destroyed during data collection, ants reconstructed them again. In 1994, dispersal date to nearby trees one month after planting a host plant inoculated with aphids was the same for all treatments (table 2). However, the number of trees with aphids was higher in plot 1 than in plot 8. This is thought to be due to the closer spacing in plot 1 and so aphids were able to escape from the ant's earth tunnels. However, the trend was more or less similar to that of 1993, i.e. many trees that were infested were in plots planted at closer spacing, under shade and without non-host plants.

Table 6. Number and species of insects/other living organisms collected from pitfall traps in 8 plots.

Order/family/common name	PLOTS							
	1	2	3	4	5	6	7	8
1 Coleoptera								
Carabus spp.	27	25	47	35	209	59	174	100
Chlaenius spp.	4	~	~	~	~	~	~	~
Other carabus	7	2	2	~	~	~	~	~
Staphylinidae	1	1	1	~	~	~	1	~
Scarabaeidae	2	1	1	~	5	8	9	13
Elateridae	2	1	1	1	~	~	~	~
Silphidae	~	3	2	6	8	23	28	76
Chrysomelidae	~	~	1	~	2	~	~	~
Cerambycidae	~	1	~	~	~	~	~	~
Curculionidae	~	~	~	~	~	~	~	~
2 Hemiptera	44	10	3	2	~	~	4	3
3 Dango mushi (Isopod)	6	~	~	~	~	1	1	~
4 Hymenoptera								
Ants	17	11	76	100	69	82	79	27
Other Hymenoptera	~	~	~	2	~	~	~	~
5 Blattaria	3	~	~	~	~	~	~	~
6 Orthoptera	12	7	75	13	55	13	47	11
7 Centipede	3	~	~	~	~	~	1	2
8 Millipede	15	13	5	10	3	6	4	4
9 Diptera	2	3	5	~	10	~	10	4
10 Lepidoptera (larvae)	~	1	1	1	~	1	1	~
11 Spider	2	8	39	17	15	10	14	~
12 Yokoebi (Amphipod)	3	1	~	7	1	2	4	8
13 Earth worm	1	1	~	~	~	1	2	3
14 Snail	~	1	~	~	~	~	1	1
15 Dragonfly (Odonata)	~	~	1	~	~	~	~	~
16 Mites	~	~	8	~	~	~	~	~
17 Geji (house centipede)	~	~	~	~	~	~	4	~
18 Un identified insect	1	~	~	~	~	~	~	~
19 Lizard	~	~	~	~	2	~	2	~

In July dispersal activities increased, and populations at each plot containing a higher proportion of immigrants fluctuated in size, possibly as a result of the balance between immigration and emigration.

New born nymphs of <u>C.todocola</u> form very compact aggregations, and have a strong tendency to maintain contact with their mother, but it was found that the 3rd instar nymphs tend to move away from the colony in which they were established. This could be due to inherent factors. Although a few alatae do emerge during the 2nd generation, in this experiment no alatae were seen. Wind direction was not found to have any relationship with dispersal or infestation. When tree conditions started to deteriorate some aphids started to move away, and although some of the trees recovered after being abandoned by aphids most of them died. It was noted that most of the dead trees were in plots planted at closer spacings and plots under shade.

Limited dispersal was observed in plots under direct sunshine, as aphid populations increased to lethal levels, plants started to deteriorate and aphid population decrease and extinction followed. The quality of food may have also caused aphids to disperse, for example tree number 12 (Table 7) in plot 1 (1994) , a month after planting had 5 aphids but after a further week all aphids dispersed, then one aphid was observed, and by the end of the month only 3 aphids remained on the plant. The opposite was observed on tree number 22. It is thought that tree number 12 was not nutritious and therefore aphids dispersed.

Dispersal was very much lower in plots that received direct sunlight, had wider spacing and were interplanted with non-host plants. In 1993 dispersal to the first tree in the plots took a longer time, compared to 1994. Therefore, the spread of aphids, and the number of the trees infested in 1994 was higher than in 1993. Maximum dispersal distance from the center tree on July 1 was observed in plots 4 and 8 (16m) in 1993 and 1994, respectively (Table 2). Dispersal distances decreased during the hot season due to high temperatures.

The effects of crowding were observed in almost all plots in August 1994, whereby population size was very low, compared with that in June/July before dispersal (Figure 1b).

Table 7. Change in aphid colony size with time in plot 1 (June,1993 and 1994).

Year/tree	No.	2,June	9,June	16,June	23,June	30, June
1993	18	(4)15,30,45,30	(4)26,39,46,39	(5)26,60,53,31,10	(6)52,47,89,46,42,4,	(6)65,97,45,100,40
"	19	–	–	-	(2)12,2	(2)24,8
		1,June	8,June	15,June	22,June	29, June 29, June
1994	6	(3),8,10,10	(3)25,20,30	(3)150,80,50	(3)1000,500,450	(5)150,1200,700,600,800
"	11	(2)15,30	(4)50,10,30,20	(3)80,100,10	(3)500,300,200	(3)600,400,1000
"	12	(1)5	no aphid	1 aphid	(1)10	3 aphids
"	16	(2)20,25	(1)44	(1)50	(1)160	(1)120
"	17	(1)16	(2)9,45	(2)50,25	(3)100,26,50	(3)50,100,200
"	18	(2)5,6	(1)30	(1)50	(1)60	(1)120
"	22	(3)50,2,25	(3)44,35,20	(3)50,20,15	(3)80,20,100	5)1000,600,500,200,1500
"	2	2 aphids	10 aphids	50 dispersed aphids	80 aphids	(2)100,350
"	28	(3)20,15,10	(3)38,7,9	(3)40,10,20	(3)50,20,45	(2)50,45
"	29	(5)50,20,5,20,20,	5 aphids	(1)20	(1)50	(2)20,25
"	7	no aphid	10 aphids	(1)20	(1)50	(2)150,100

( )=Number of colony per tree.

Rate of population increase (Figure 2) was calculated as $Log=(N_{t+1}/N_t)$

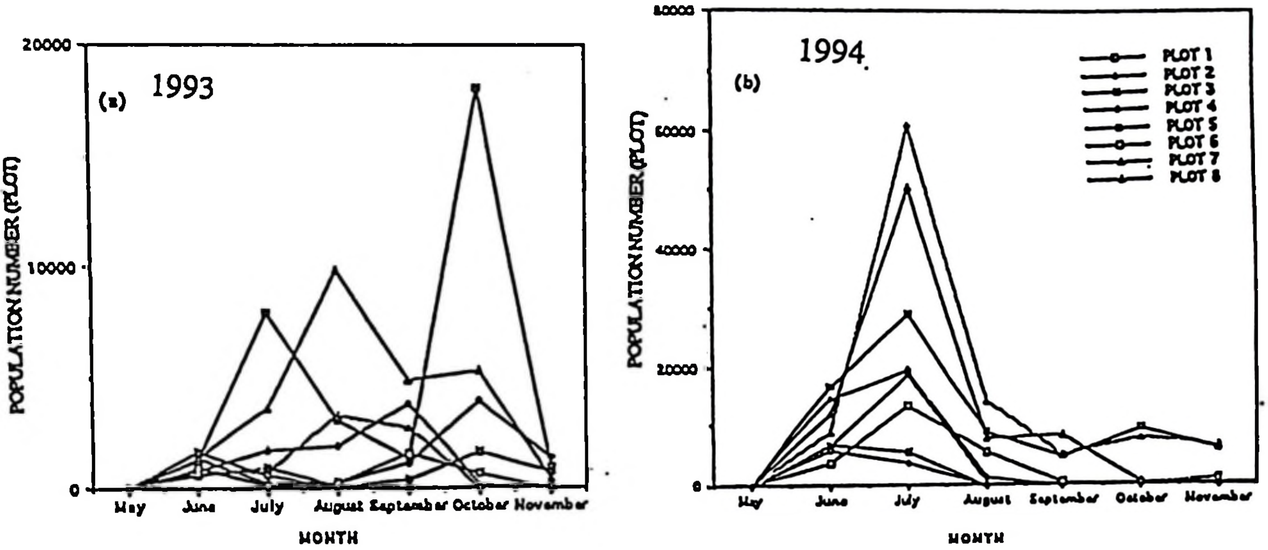


Figure 1. Cinara todocola population size in 1993 and 1994.

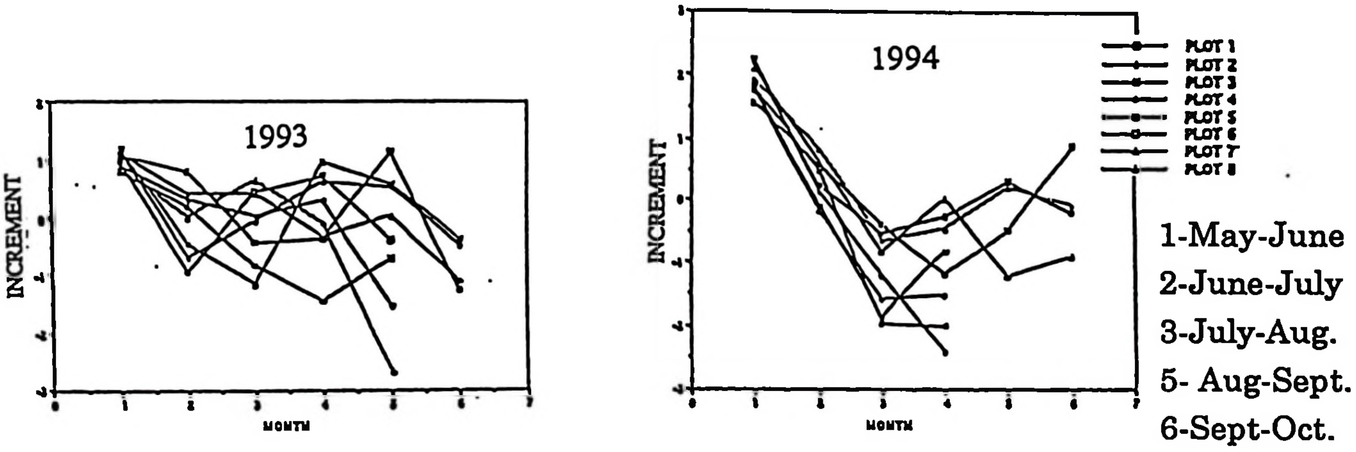


Figure 2. The rate of population increase in 1993 and 1994 (Log.).

Rate of increase=Log (Nt+1/Nt)

2.5.2 Population growth

Population growth of aphids per plot is shown in table 8. In general population size per plot and the number of trees infested was higher in 1994 than in 1993. However, the mortality rate of trees infested with aphids was higher in 1993. This was due to the fact that aphid populations concentrated on only a few trees and did not disperse until the tree's condition deteriorated or it died. Colonies attended by ants had higher population growth rates compared to unattended ones. In general high population growth was observed in June and July (1993) and in September and October (1994). This also influenced dispersal rate. About 64% and 42% of trees infested by aphids died in 1993 and 1994, respectively.

Table 8. Population growth (number of individuals) of C.todocola per plot in 1993 and 1994.

Plot No./year		MONTH						
		May	June	July	August	September	October	November
1	1993	100	1225	7974	3110	13666	18105	995
	1994	100	16723	38904	8694	4772	9530	5960
2	1993	100	816	1714	1926	3844	115	0
	1994	100	14821	19591	1220	5	0	0
3	1993	100	1630	626	45	418	1651	730
	1994	100	6563	5586	75	12	0	0
4	1993	100	1400	300	265	1137	4015	1400
	1994	100	5739	3774	98	3	0	0
5	1993	100	633	950	143	5	1	0
	1994	100	6365	18771	202	2	0	0
6	1993	100	930	106	295	1615	680	0
	1994	100	3588	13447	5595	365	123	940
7	1993	100	721	730	3330	2718	8	0
	1994	100	8633	60681	14044	5052	7880	6486
8	1993	100	1371	3670	9922	4945	5334	430
	1994	100	11929	50417	7822	8360	497	63

An aphid population started as a small colony of 3-4 aphids, then grew into a very huge one with about 1500 aphids in some cases, as shown in Table 7. For example, tree number 22 in 1994 started with 77 aphids in 3 colonies on June 1 and ended with 3800 aphids in 5 colonies. The effect of food quality on population growth is shown by tree number 29 in 1994 where population growth on this tree was stagnant, starting with 125 aphids and ending with 45 aphids, and by tree number 12 where aphids visited the plant and left. Thus aphids tended to colonize on the more vigorous shoots. This species is a phloem feeder and prefers young plant parts, it first attacks thick young branches then moves to thinner ones. Aphids born during the first generations are large and heavy compared to those born during later generations (Table 9). Third instar nymphal weights were taken at the end of each month from May through October. There was a highly significant difference between months. An adhoc-test was used to determine which month weights differed significantly. Probabilities greater than 0.003 (0.05/11tests) were assumed to be significantly different, in a Tukey multiple comparison test.

July weights were higher than those of June, and this can be explained by a reduction in intraspecific competition and space created after dispersal. Therefore, crowding and food quantity/quality may affect aphid body size. Aphids feeding on weak plants initially ingested phloem sap, but then suddenly withdrew their stylets and left the plant. Such observations have lead to the suggestion that the phloem sap of weak plant species is nutritionally unsuitable or may not contain enough nutrients needed by the insects. Morishita's aggregation index (Morishita, 1968) values in table 10 were greater than 1 in all treatments which means that aphids showed a contagious distribution. The density, abundance and infestation rate of aphids were calculated using Furuta's (1976) method. Density = X/N1: where X is the total number of individuals of <u>C.todocola</u> in the experimental plot, N1 is the number of trees in the plot. Abundance = X/N2 : where N2 is the number of trees in the plot on which infestations of <u>C.todocola</u> were observed. Then infestation rate = N2/N1x100. Tables 11, 12, and 13 show aphid density, abundance, and infestation rate in different plots for 1993 and 1994.

Table 9. Weight of aphids born during initial and last generations in 1994.

Month	n	Min-Max(g)	X±SD(g)
May	32	0.0014-0.0030	0.0025±0.0005
June	43	0.0011-0.0033	0.0020±0.0007
July	8	0.0014-0.0030	0.0023±0.0005
Aug.	43	0.0008-0.0033	0.0019±0.0006
Sept.	20	0.0010-0.0030	0.0018±0.0006
Oct.	16	0.0011-0.0021	0.0016±0.0003

Analysis of variance of the effect of time on 3rd instar nymphs were highly significant (F=9.515 df=5,152, P<0.0001).

Tukey multiple comparisons, matrix of pairwise comparison probabilities

	May	June	July	August	September	October
May	1					
June	0.00239	1				
July	0.63186	0.98098	1			
Aug.	0.84696	0.00004	0.23287	1		
Sept.	0.11961	0.0002	0.02535	0.56715	1	
Oct.	0.11951	0.0002	0.02535	0.56715	1	1

Calculated significant probability level= 0.003 (0.05/15tests)

The rate of infestation was very high in plot 1 (1993) and plot 7 (1994). Dense colonies of aphids were observed on trees with ant nests, which in some how prevented their dispersal and attack by natural enemies. As the reproductive capacity of this aphid is very high, dense colonies were formed on trees soon after adults started to reproduce.

Table10. Morishita aggregation index for 1993 and 1994.

Plot No./year		MONTH						
		May	June	July	August	September	October	November
1	1993	0	33.5	10.46	11.41	30.09	14.44	23.77
	1994	0	33.6	31.71	12.63	10.02	9.51	31.15
2	1993	0	24.33	12.65	15.17	25	-	-
	1994	0	24.33	8.43	13.59	7.85	20.69	-
3	1993	0	36	25.05	34.46	35	35	-
	1994	0	35	35	35	34.19	21.86	35
4	1993	0	35	23.35	24	24	-	-
	1994	0	35	35	35	32.63	17.08	24
5	1993	0	25	23.84	25	25	-	
	1994	0	26	25	25	25	25	
6	1993	0	25	11.73	19.29	19.02	25	25
	1994	0	25	25	25	25	25	
7	1993	0	21	5.43	10.95	15.35	11.1	15.29
	1994	0	21	21	21	21	21	-
8	1993	0	25	6.95	12.66	19.49	19.98	25
	1994	0	25	7.85	10.67	20.31	14.06	12.08

Table 11. Aphid density per plot in 1993 and 1994.

Plot No.		Month						
		May	June	July	August	September	October	November
1	1993	0.71	8.75	56.96	22.21	7.59	133.12	10.58
	1994	0.71	90.39	277.88	49.12	38.08	76.85	48.85
2	1993	1	8.16	17.14	19.26	30.75	1.15	
	1994	1	118.57	19.59	10.43	0.05		
3	1993	0.71	11.64	4.47	0.32	2.26	11.79	7.16
	1994	0.71	35.47	39.9	0.41	0.09		
4	1993	1.04	14.58	3.12	2.76	9.47	41.82	13.72
	1994	1.04	47.82	39.31	0.84	0.03		
5	1993	1	6.33	9.5	1.43	0.04	0.01	
	1994	1	50.92	187.71	1.62	0.02		
6	1993	1	9.3	1.06	2.65	13.46	6.8	
	1994	1	31.1	134.47	44.76	3.65	1.25	7.52
7	1993	1.19	8.58	8.69	39.64	25.88	0.07	
	1994	1.19	82.21	723.39	143.31	70.17	109.44	72.07
8	1993	1	13.71	36.7	99.22	41.21	55.56	6.06
	1994	1	95.43	504.17	62.58	83.6	5.07	0.52

Tabale 12. Aphid abundance in 1993 and 1994.

Plot No./year		May	June	July	August	September	October	November
1	1993	100	175	613	115	37	647	142
	1994	100	316	828	170	393	794	596
2	1993	100	136	156	137	192	23	
	1994	100	353	490	49	5		
3	1993	100	326	156	11	60	206	730
	1994	100	437	698	12	6		
4	1993	100	280	75	66	227	502	1400
	1994	100	717	472	20	3		
5	1993	100	127	237	36	5	1	
	1994	100	490	2681	674	2		
6	1993	100	186	26	74	323	227	
	1994	100	87	896	466	37	31	313
7	1993	100	144	182	832	544	6	
	1994	100	345	1785	562	505	985	811
8	1993	100	274	229	620	309	667	215
	1994	100	519	2653	434	760	83	31

Table 13. Aphid infestation rate (%) in 1993 and 1994.

Plot No./year		MONTH						
		May	June	July	August	September	October	November
1	1993	1	5	9	19	20	20	7
	1994	1	29	33	29	10	10	10
2	1993	1	6	11	14	16	5	0
	1994	1	33	40	21	1	0	0
3	1993	1	3	3	3	4	6	1
	1994	1	8	6	3	1	0	0
4	1993	1	5	4	4	4	8	0
	1994	1	7	8	4	1	0	0
5	1993	1	5	4	4	1	1	0
	1994	1	10	7	2	1	0	0
6	1993	1	5	4	4	4	3	0
	1994	1	33	15	10	10	4	2
7	1993	1	6	5	5	5	1	0
	1994	1	24	40	25	14	11	9
8	1993	1	6	16	16	13	8	3
	1994	1	18	19	14	11	6	2

From mid-October immature male aphids were observed in some colonies. Table 14 shows the percentage of males produced per tree in 1993 and 1994. Production of males started 6 days earlier in 1993 than in 1994. There was a significant positive relationship between the number of males produced to the total number of individuals in a colony (Figure 2b). C.todocola showed the following population growth patterns; populations with only one peak, e.g. plots 2,3,4,5 and 6 (1994) and plot 5 (1993); population with two sharp peaks e.g. plot 1 (1993/94), and populations with two low peaks as in plot 2 (1993). With two-peak populations the first peak was in June/July and the second peak was in September /October. It was sometimes observed that when the first peak was low the second one was high or vice versa as observed in plot 1 in 1993/94 (Figures 1, 6). Peaks were followed by migration. Dispersal of aphids created space and reduced competition for those remaining and this encouraged further population growth of those remaining since aphids are opportunists. It can be said that high population densities influenced dispersal.

In summary, the following population growth characteristics were noted:-

-Clumped spatial distribution within some plots.

-Steep and steady population growth that enabled the insect to increase to destructive levels despite low initial densities.

-Violent fluctuations of the population density within a plot.

These characteristics may have resulted from the combinations of the physiological traits intrinsic to the insect and the environmental conditions.

Table 14. Percentage of immature sexual male production over time in 1993 and 1994.

		DATES					
Year/plot	No.	20.Oct	27.Oct	6.Nov	10.Nov	17.Nov	
1993	1	–	–	(60)16	(105)27	(6)9	
•	2	(63)7	–	–	–	–	
•	3	(8)16	(29)5	(36)5	(42)9	(6)9	
•	4	(65)6	(148)31	(160)7	(70)10	syrphid larva	
•	5	–	–	–	–	–	
•	6	(2)1	–	–	–	–	
•	7	–	–	–	–	–	
•	8	–	–	–	–	–	
		26.Oct	2.Nov	7.Nov	30.Nov	7.Dec	14.Dec
1994	1	(19)12	(108)8	(333)20	(271)32	(252)8	(431)19
•	6	-	(11)11	(49)9	-	-	-
•	7	(42)30	(262)17	(524)26	-	(85)22	(62)52

( )=Number of immature males per group of aphids with males.

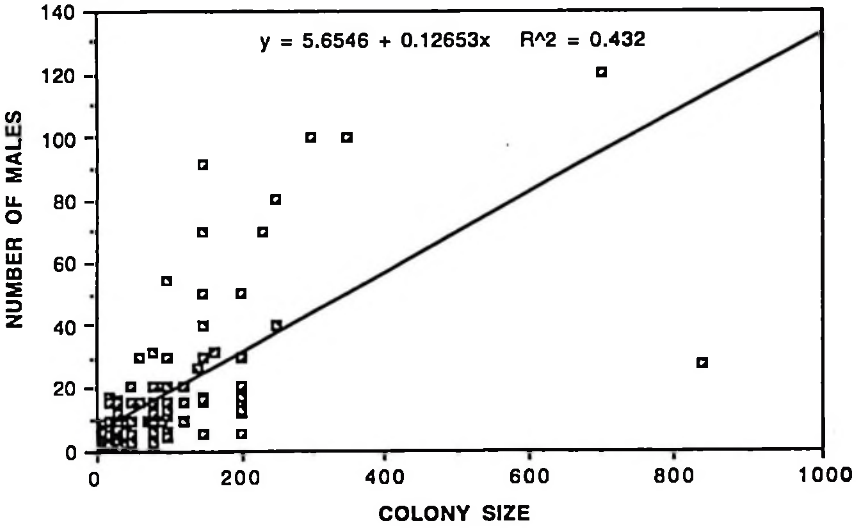


Figure 2c. The relationship between the number of males to colony size of C.todocola in 8 treaments in 1993 and 1994.

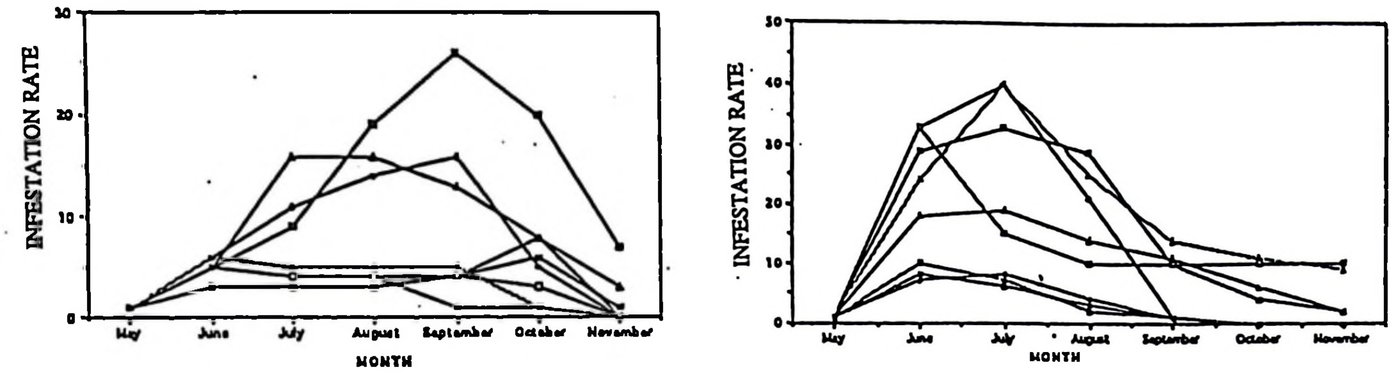


Figure 3. Infestation rate of aphid on host plant in 1993 and 1994.

Infestation rate=N2/N1

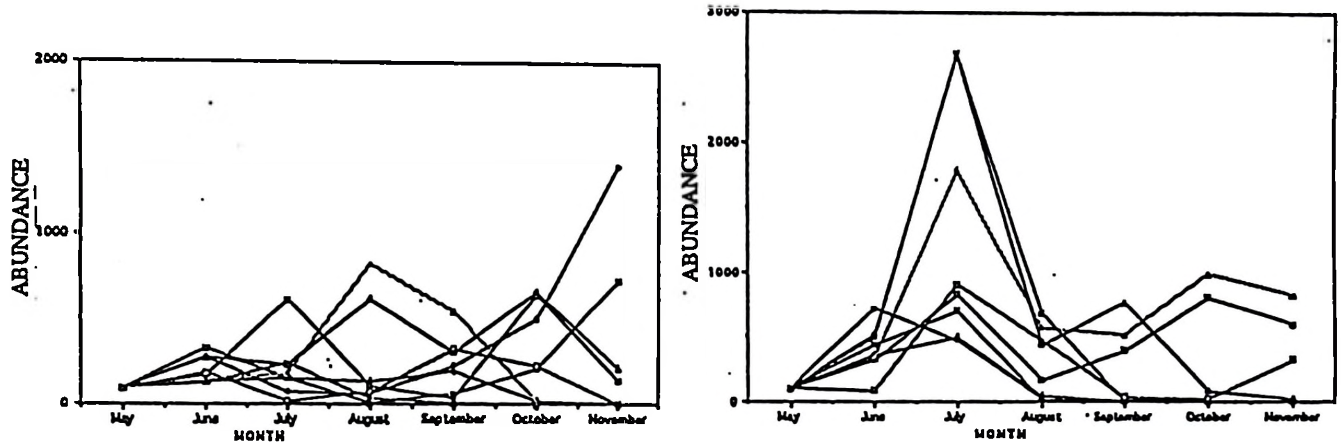


Figure 4. Aphid abundance in 1993 and 1994.

Abundance=X/N2

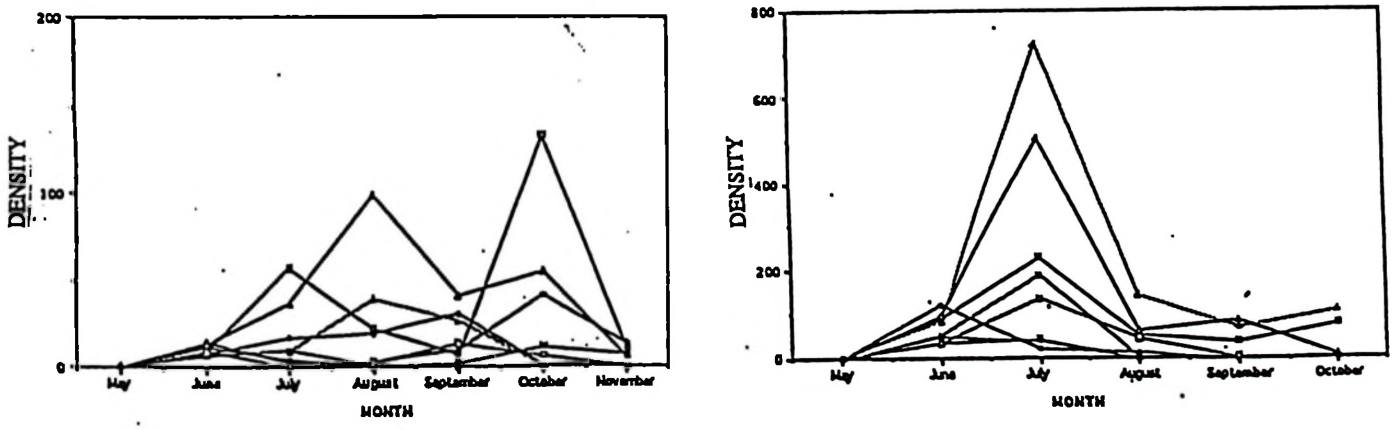


Figure 5 . Aphid density in 1993 and in 1994.

Desity= X/N1

2.6 POPULATION DYNAMICS AND DISPERSAL IN EACH PLOT

Comparisons on the infestation rate, abundance and density of C.todocola in 8 plots over two years is shown in figures 3, 4 and 5, respectively.

Plot 1

Aphids were found to disperse to nearby trees in this plot earlier than in the other plots. One month after planting the tree with 100 aphids at the center of the plot, only one other tree had aphids in 1993 and 10 other trees in 1994.

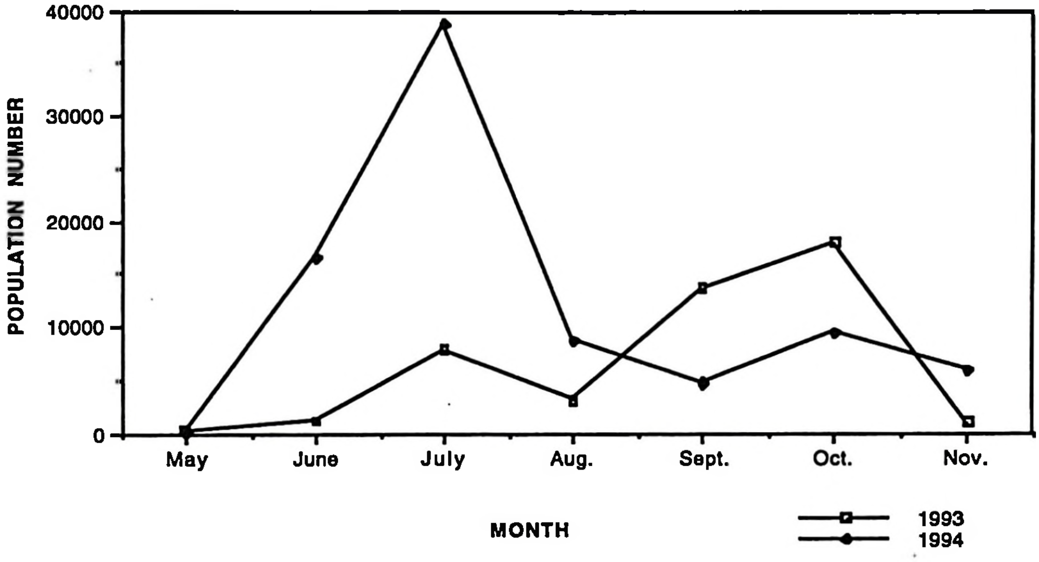


Figure 6. Population growth in plot 1 in 1993 and 1994 (corresponding to Table 8).

Maximum distance traveled by aphids during initial dispersal was 2m and 5.66m in 1993 and 1994, respectively (Table 2). Their movement was mainly caused by population pressure at this stage. However, deterioration of the host plant quality, presence of predators and high temperatures influenced dispersal at a later stage. Total number of trees with aphids in 1993 was 9 while in 1994 it was 14 (Table 5).

Aphid population number per plot peaked in September and October in 1993 (n=13666 and 18105 respectively), and June and July in 1994 (n=16723 and 38904 respectively). Figure 6 shows population growth in plot 1, and figure 2 shows the rate of population increase { (rate of increase =log(Nt+1/Nt). Population growth was characterized with two peaks, one in July and the other in

October in both years. Intra-tree movement was also noticed. Table 8 shows change in numbers and colony size within a tree in 1993 and 1994. Detailed studies on aphid movement within a tree is dealt with in chapter 3. Maximum number of aphids per colony were 1500 (1994 June, 29) along the stem of tree number 22, and 100 aphids (1993 June, 30) on plant number 18. Difference in number of aphids on trees can give some explanation on the host quality.

All trees infested with aphids were found to be attended by ants (Lasius hayashi) in both years. About 67% and 50% of the trees infested with aphids died in 1993 and 1994, respectively. Figure 7 shows that infestation rate was higher in 1994 than in 1993. In 1993 infestation peak was attained in September compared with July in 1994.

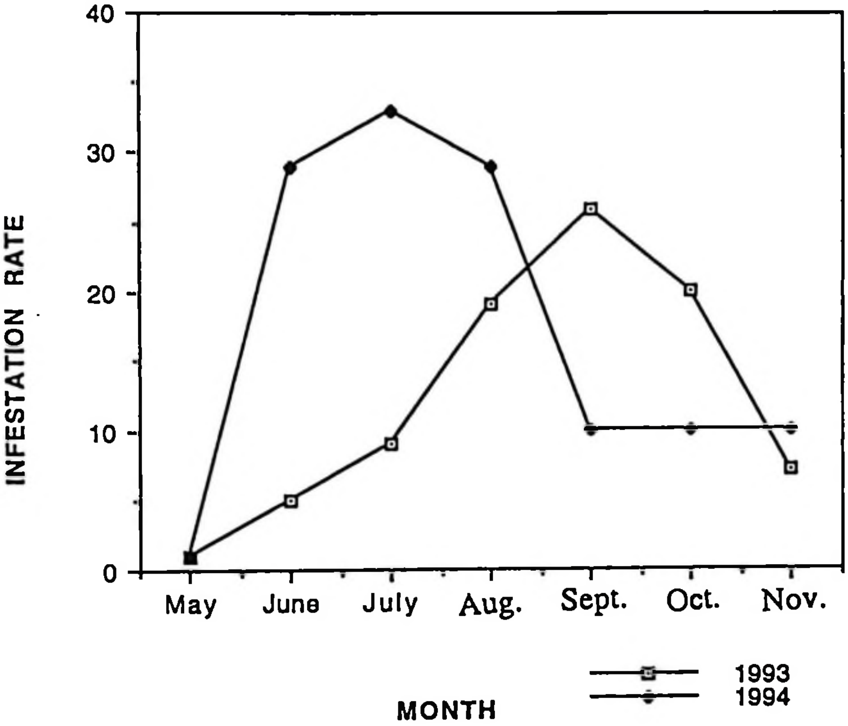


Figure 7. Infestation rate in plot 1 in 1993 and 1994.

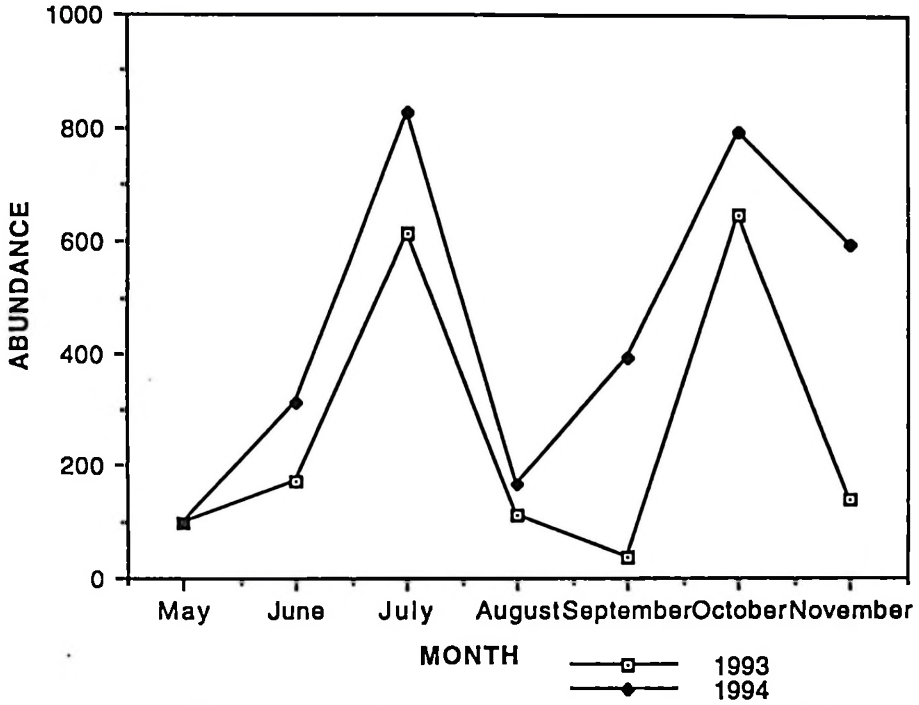


Figure 8. Aphid abundance in plot 1 in 1993 and 1994

Maximum abundance was observed in October 1993 and in July 1994, however the pattern was more or less similar for both years (Figure 8). High densities were found in October 1993 and July 1994 (Figure 9).

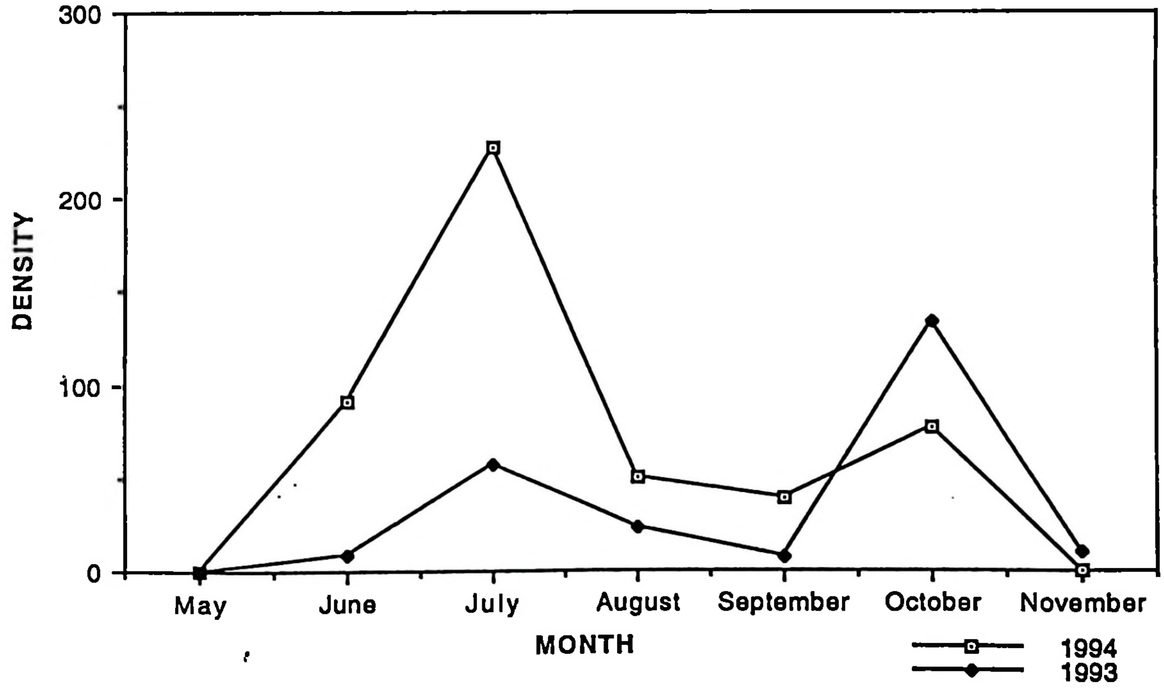


Figure 9. Aphid density in plot 1 in 1993 and 1994

Aggregation values per month for 1993 and 1994 are shown in figure 10 not all trees with aphids were attended by ants (Table 4). Hunting spiders were the most common predator of aphids. Lady bird beetles and syrphid larvae were also observed in this plot. Wasps were also noticed flying around, but were not observed to prey on aphids.

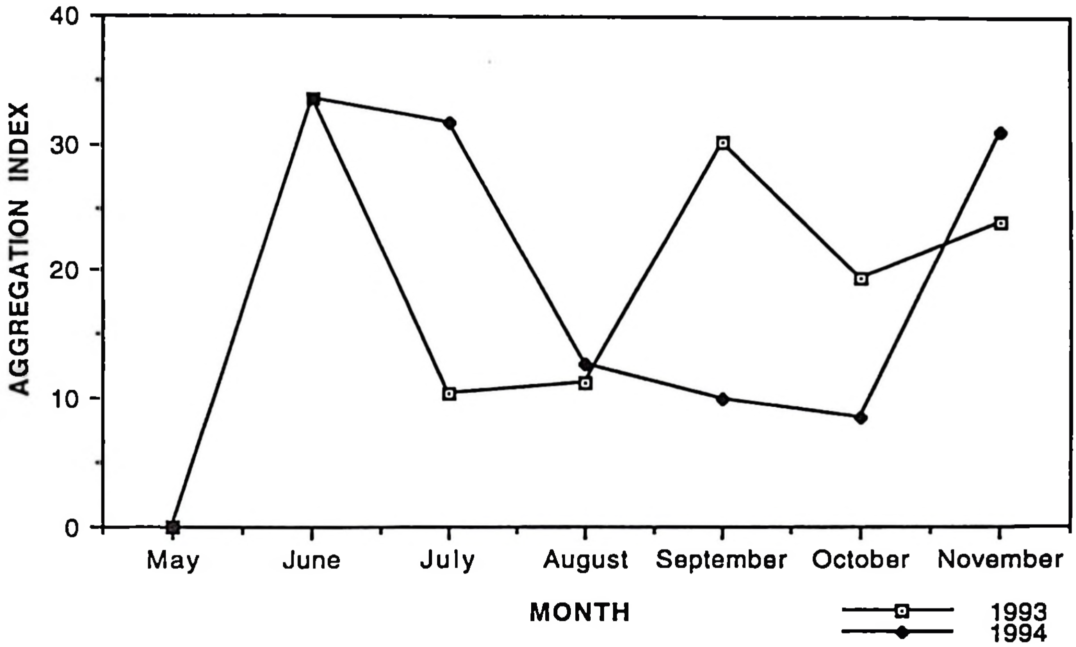


Figure 10. Aphid aggregation index in plot 1 in 1993 and 1994

Plot 2

Dispersal of aphids in this plot was higher in 1994 than in 1993. Maximum initial dispersal distance was 4m in 1993 and 5.66m in 1994. Figure 11 shows that the population growth was characterized by a single peak and, after maximum population was reached, a sharp drop in population occurred. The rate of population increase, decreased after the population peak (1994) as observed in Figure 2. Ants nests, planting distance and interplanting with a non-host plant species may have some impact on the dispersal. In 1993 aphids dispersed into one tree only, but in 1994 into 7 trees.

Ants were found on amost all trees with aphids in 1993 and 73% of trees with aphids in 1994. It is assumed that the quality of honeydew produced by aphid colonies not attended by ants are of lower quality. On the other hand 40% and 18% of trees with aphids died in 1993 and 1994 respectively. Figure 12 shows that infestation rate in June, July and August, 1994 was higher than that in 1993.

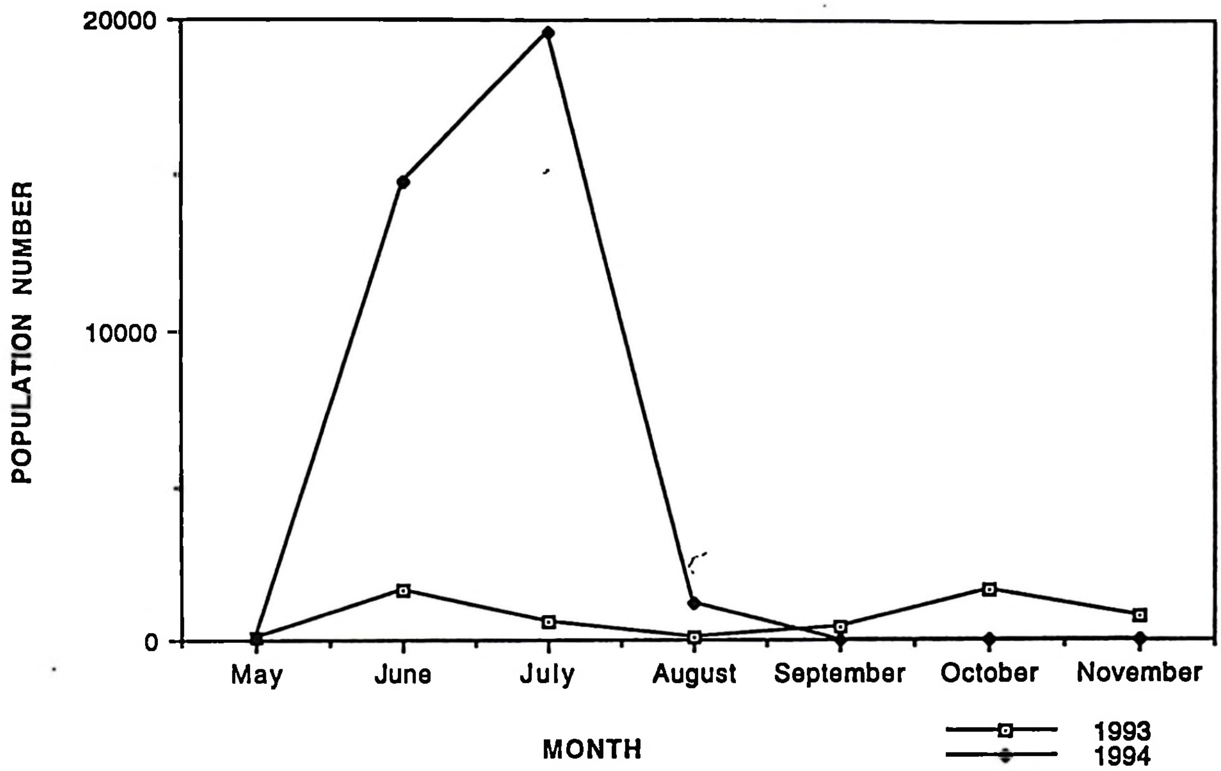


Figure 11. Population growth in plot 2 in 1993 and 1994

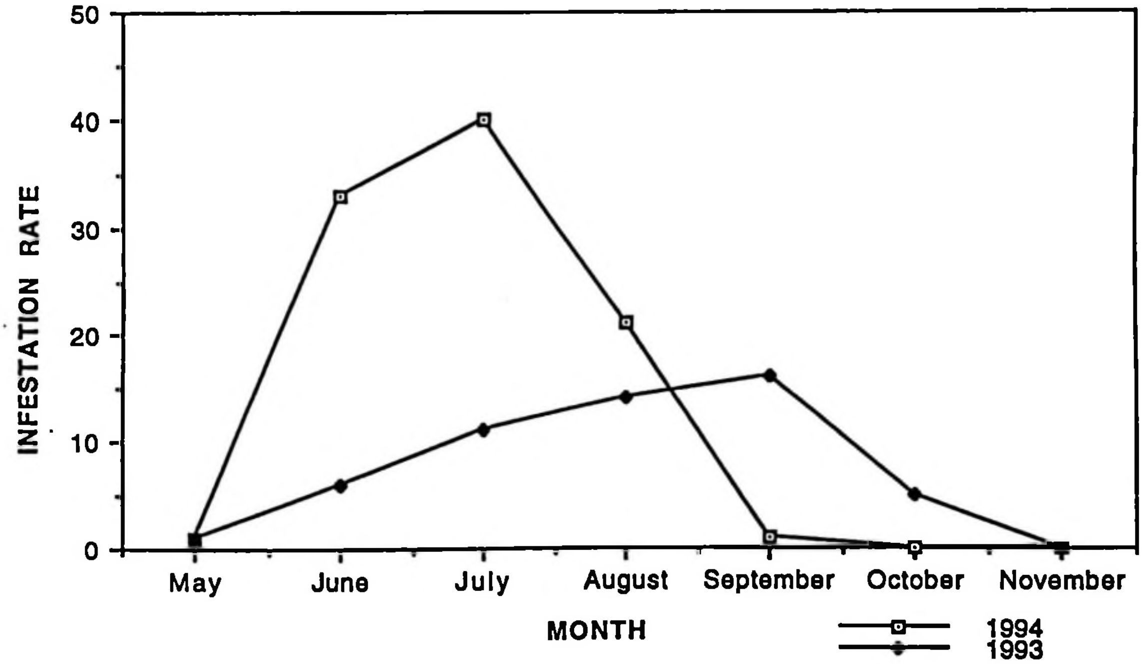


Figure 12. Infestation rate in plot 2 in 1993 and 1994.

Aphid abundance reached its peak in July, 1994 and then dropped drastically, while in 1993 there was a more or less steady increase until September which then started to descend (Figure 13).

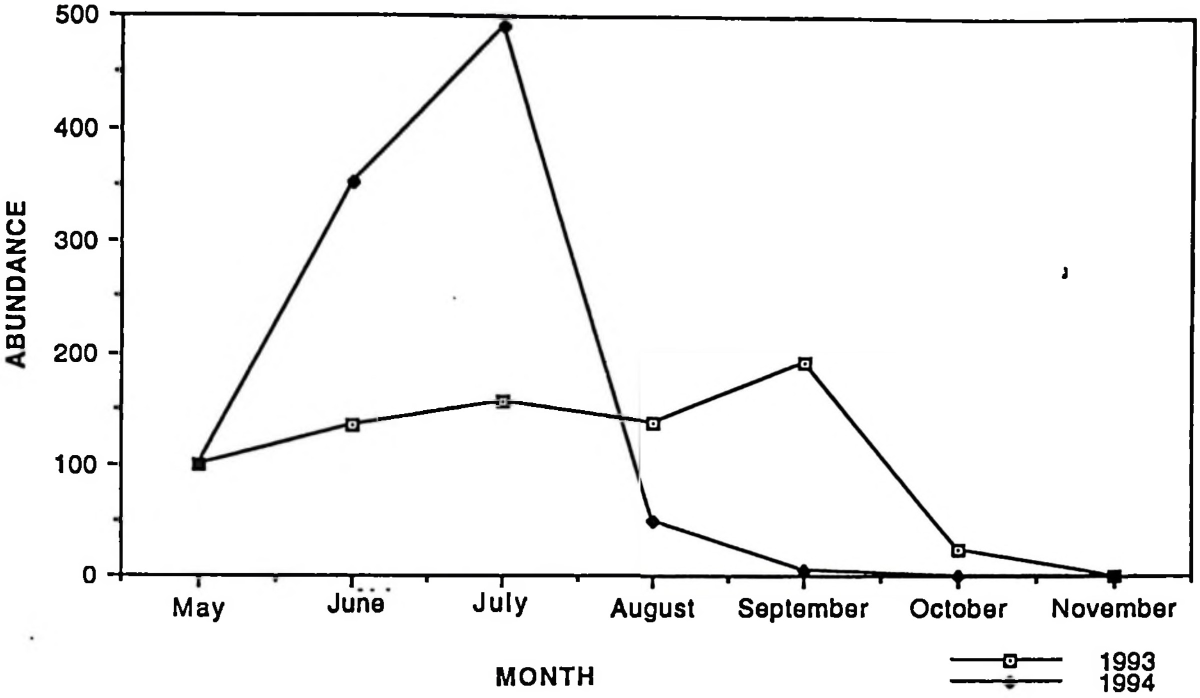


Figure 13. Aphid abundance in plot 2 in 1993 and 1994.

Aphid density in 1993 showed a gradual increase, while in 1994 the population collapsed in September after a steep increase as shown in figure 14. Figure 15 shows higher aggregation index values in 1993 compared to 1994.

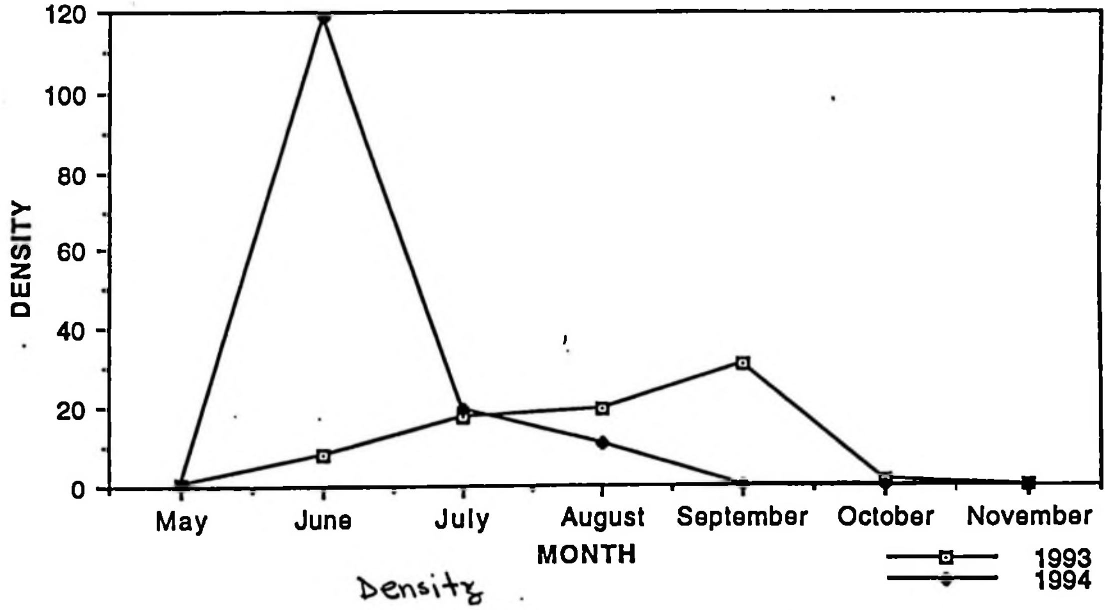


Figure 14. Aphid Density in plot 2 in 1993 and 1994.

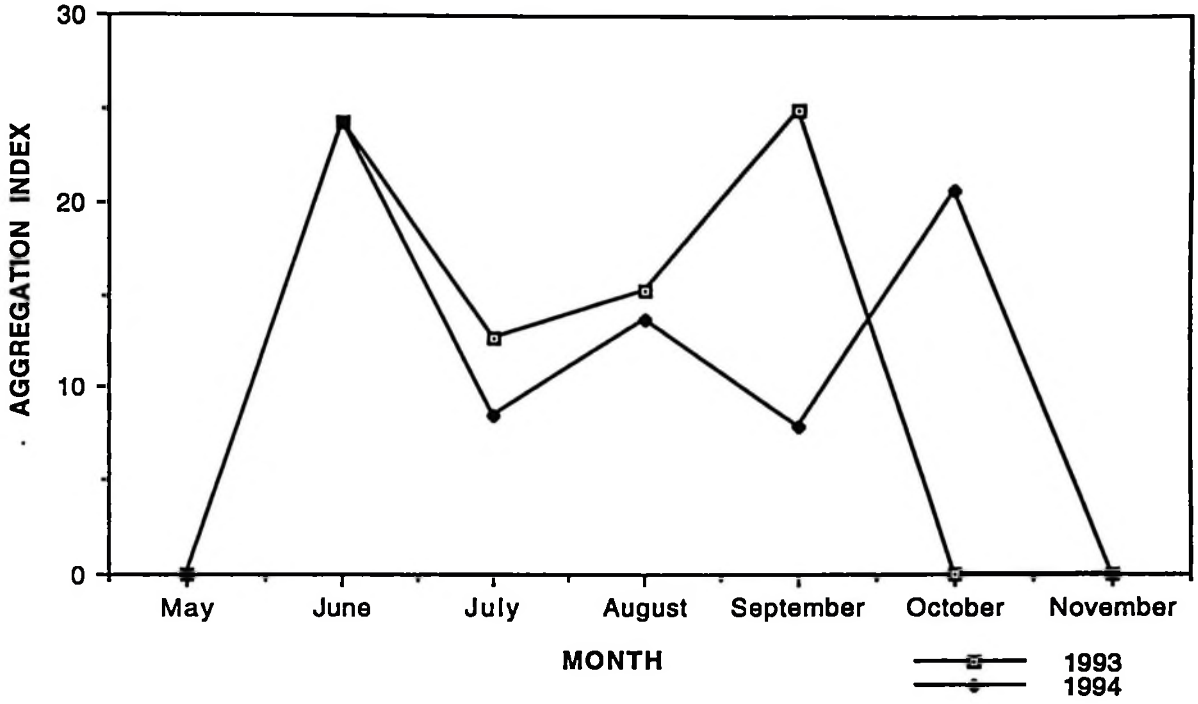


Figure 15 Aphid aggregation index in plot 2 in 1993/1994

Some of the trees were infested with spittle bugs, and aphids abandoned those trees.

Plots 3,4,5,6 and 7

These plots have one thing in common, that is, part or the whole plot received sunlight. Initial spread of the aphids was very low. In plots 5,6 and 7, aphids remained on the center tree and did not move at all in 1993. Population growth of aphids in the 5 plots is shown in figure16. Population growth was characterized by a single peak in 1994 and a low level double peak in 1993, except for plot numbers 5 and 7. The rate of population increase is shown in figure 2 where a drastic decrease was observed in 1994.

Ants species associated with these aphids are shown in table 3. Percentage of trees with aphids attended by ants is shown in table 4, while percentage of dead trees infested with aphids is shown in table 5. Higher values of infestation rates (Figure17) were observed in 1994 in general. Aphid abundance (Figure 18) fluctuated with time especially in plots 6 and 7. Aphid density (Figure 19) was higher in 1994 but around October 1993 higher values were observed in plots 3,4 and 6. A lower aggregation index value was observed in July 1994 (Figure 20).

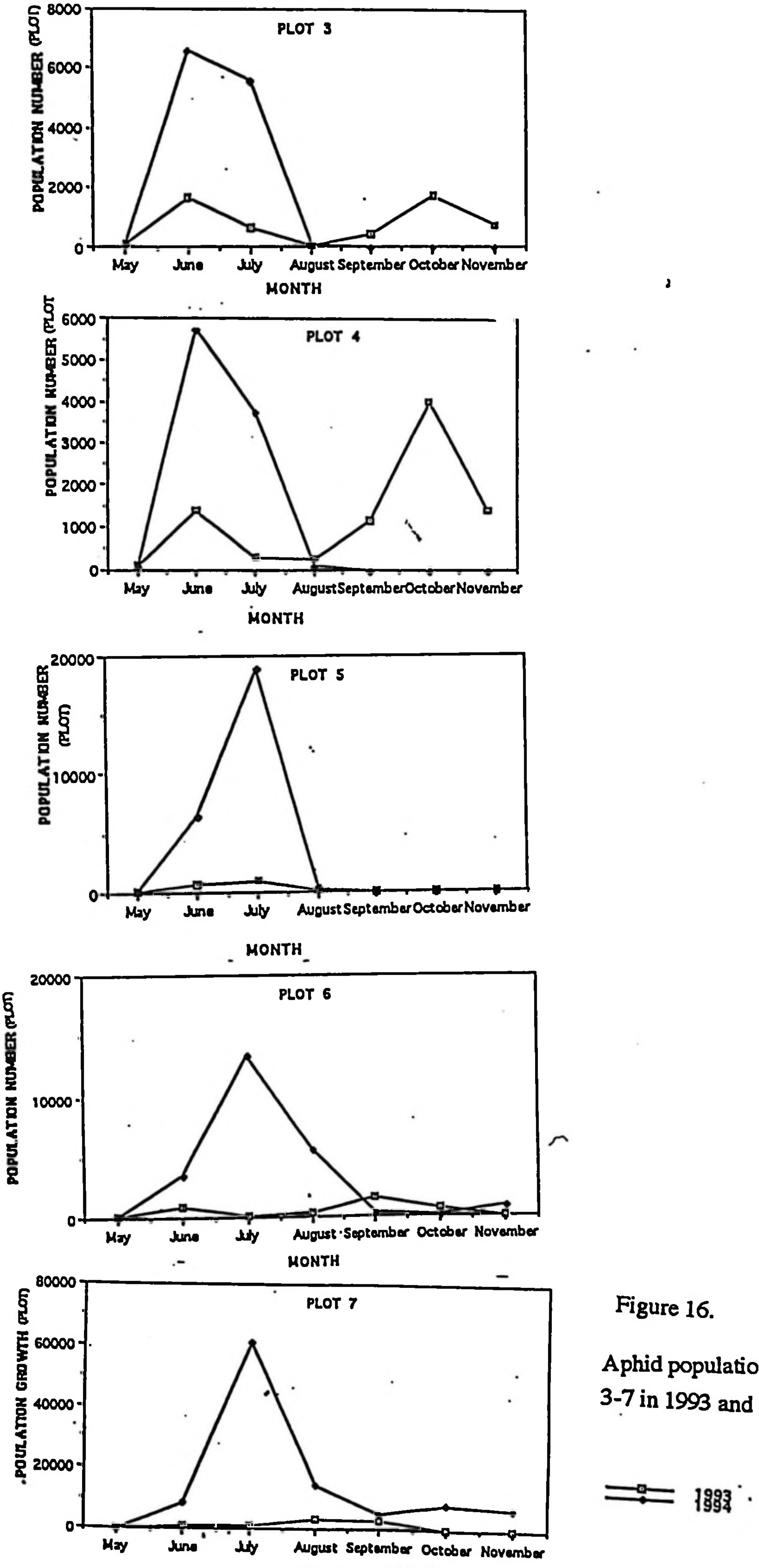


Figure 16.

Aphid population growth in plots 3-7 in 1993 and 1994.

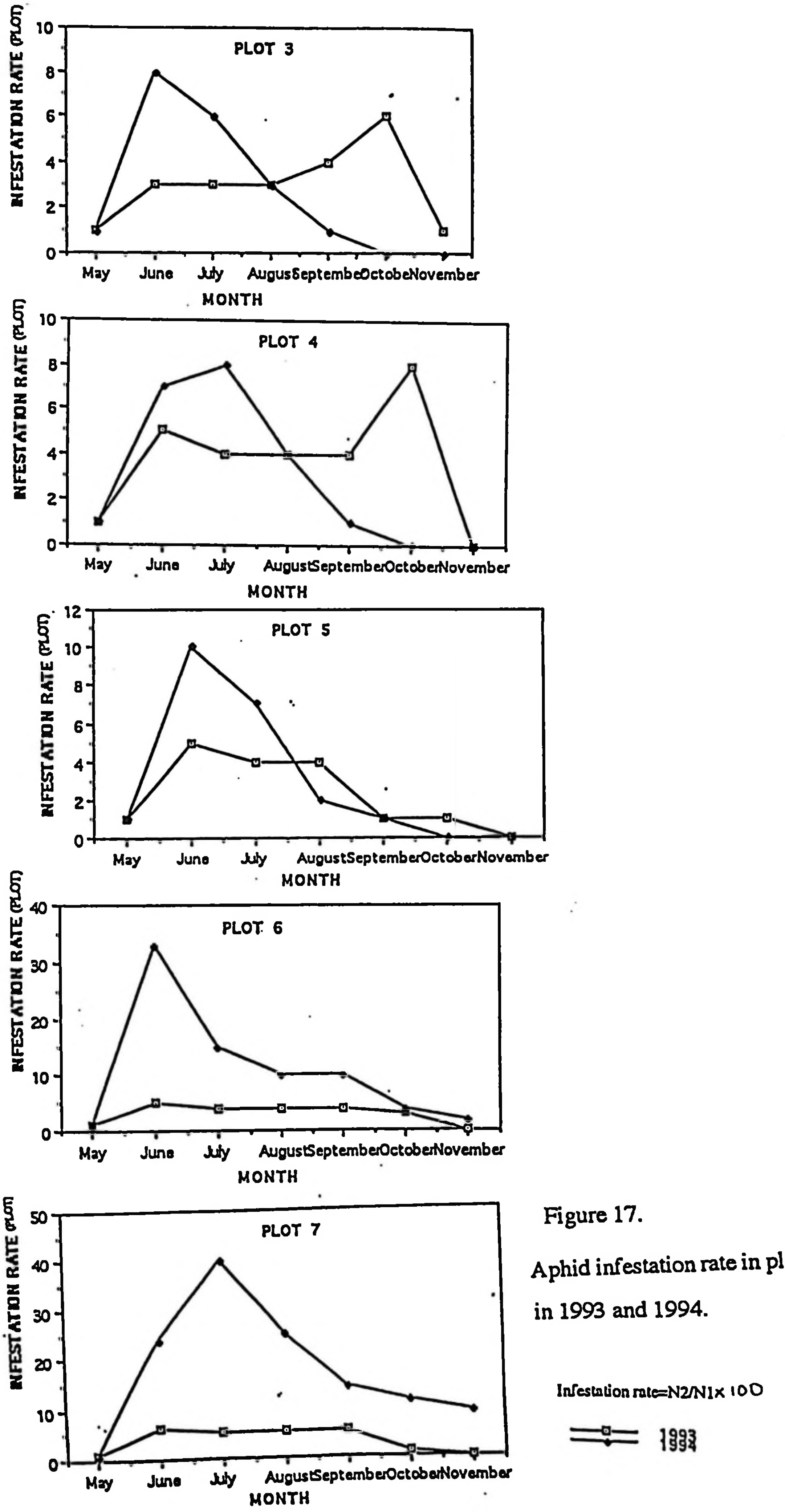


Figure 17.

Aphid infestation rate in plots 3-7 in 1993 and 1994.

Infestation rate=N2/N1× 100

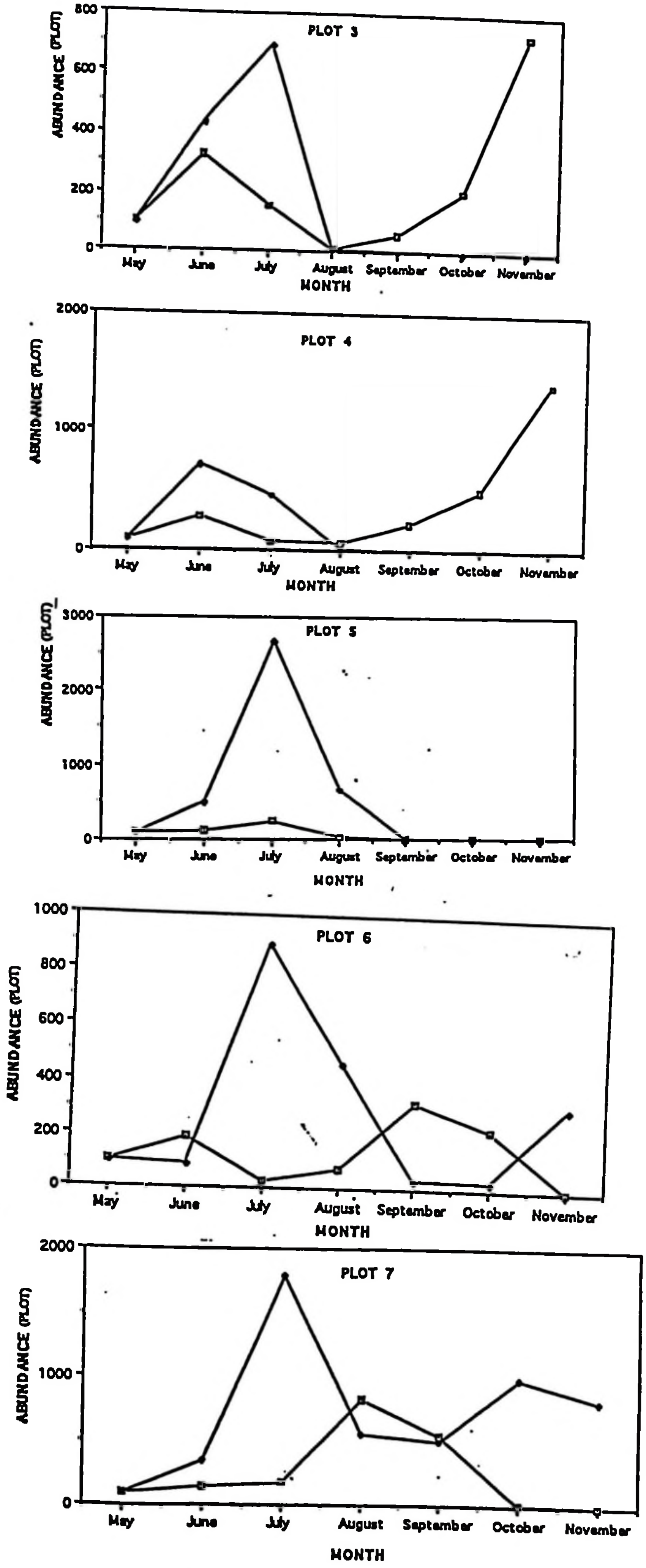


Figure 18.

Aphid abundance in plots 3-7 in 1993 and 1994.

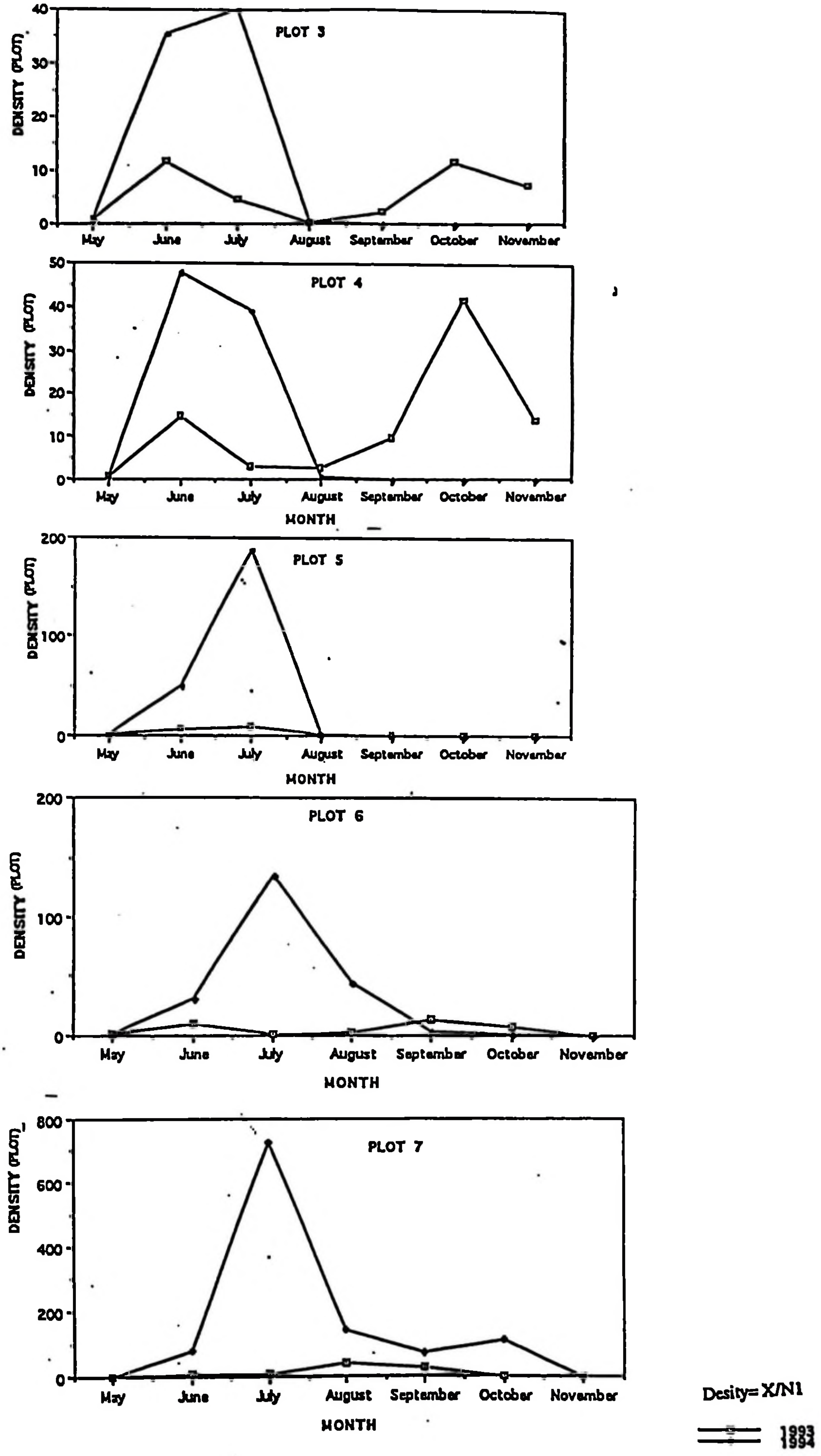


Figure 19. Aphid density in plots 3-5 in 1993 and 1994.

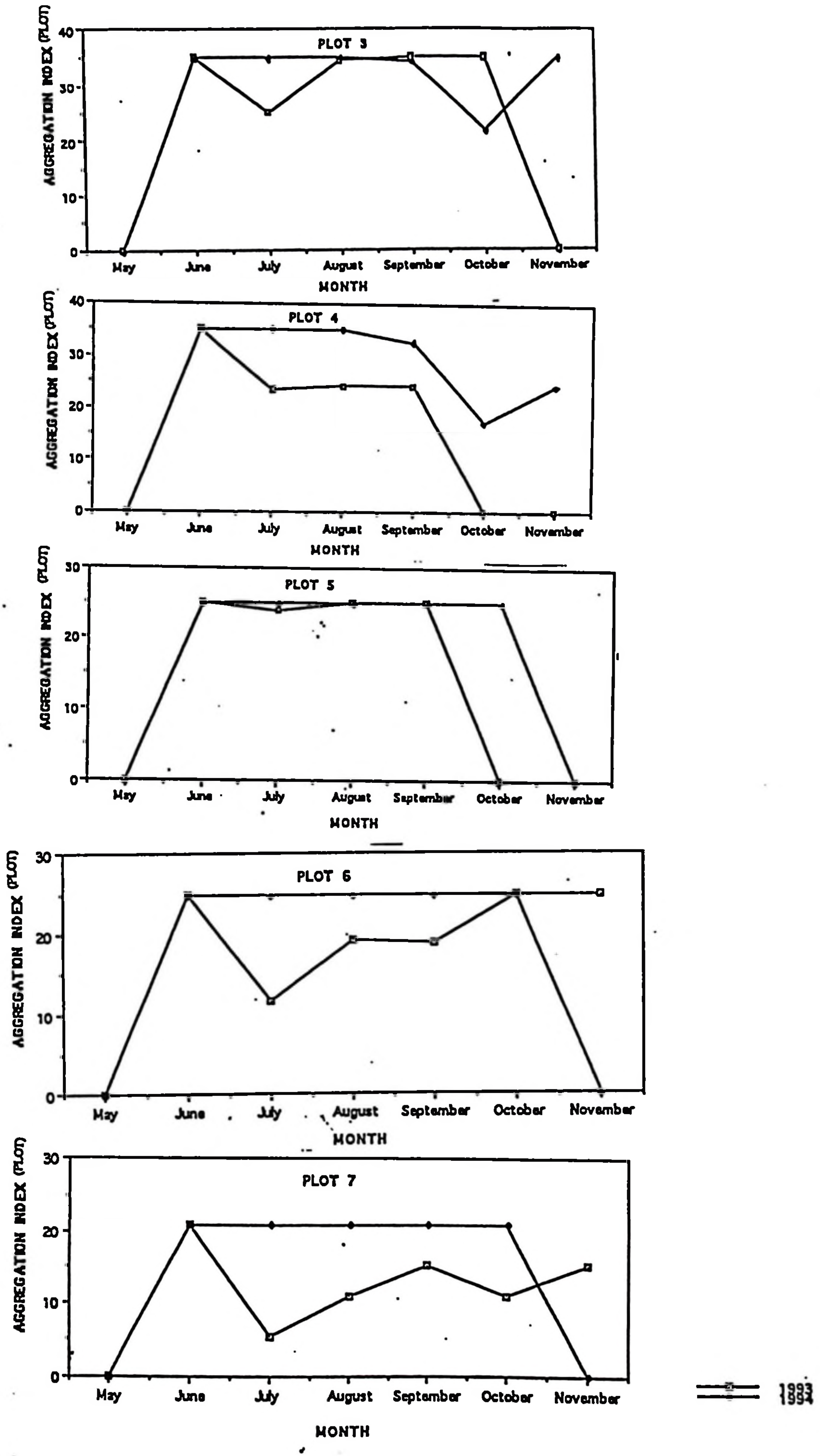


Figure 20. Aphid aggregarion index in plots 3-7 in 1993 and 1994.

Plot 8

Initial dispersal was faster in 1993 but final number of trees with aphids was the same, at 7 trees (Table 2). Maximum dispersal distance was 16m and 5.66m in 1993 and 1994, respectively. Population growth as shown in figure 21 is characterized by two peaks, and the rate of increase is shown in figure 2. Figure 22, 23, 24 and 25 show aphid infestation rate, abundance, density and aggregation in plot 8 respectively.

However, the population size in 1994 was larger than that in 1993. About 85% and 57% of the trees with aphids were attended with ants in 1993 and 1994 respectively, and 71% of these trees died in 1993 and 14% in 1994. Infestation rate was higher in 1994 as seen in Figure 22, while aphid abundance and density fluctuated as shown in figures 23 and 24. Aggregation index was lower in July in both years (Figure 25).

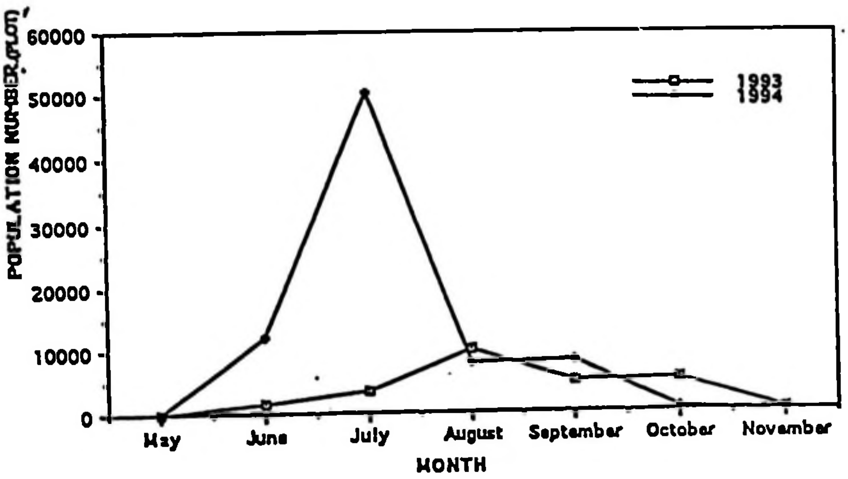
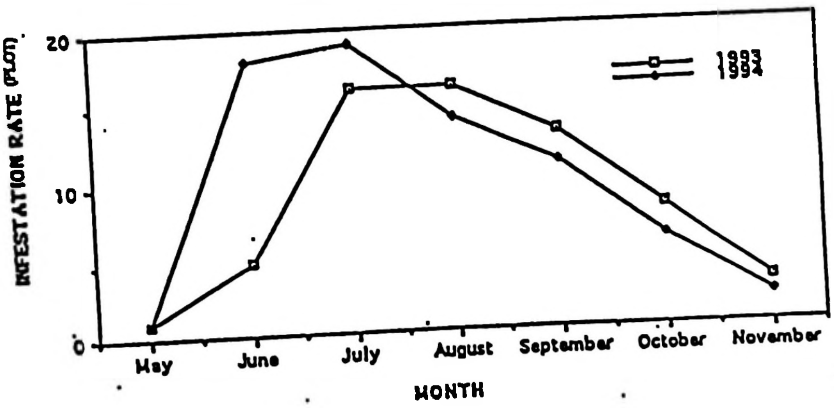
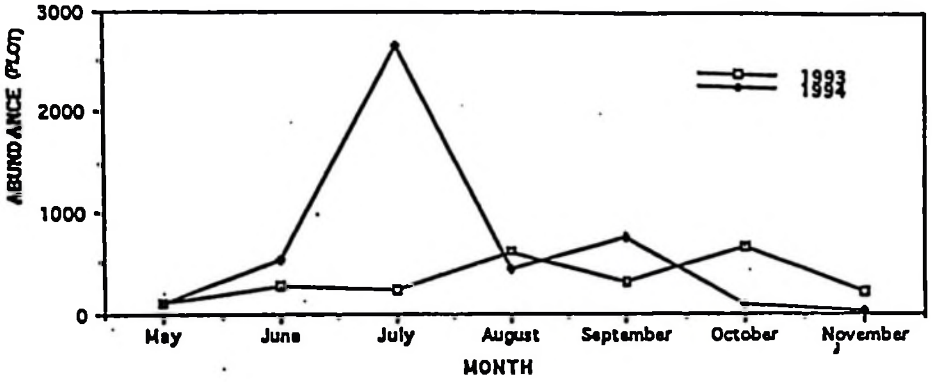


Figure 21. Population growth of C.todocola in plot 8 in 1993 and 1994.



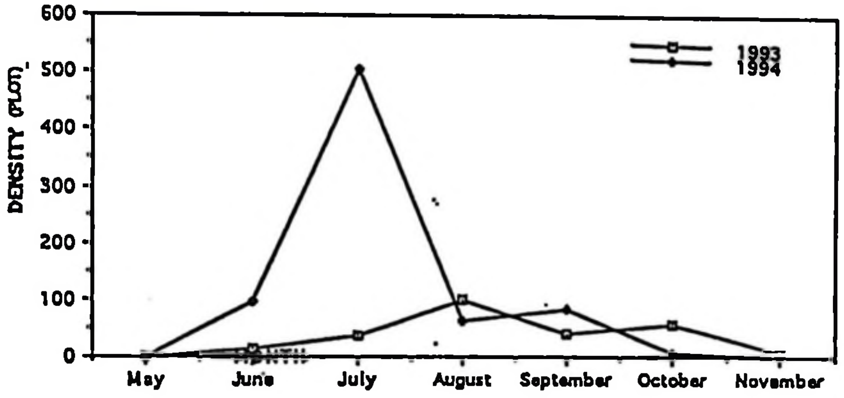
Infestation rate=N2/N1×100

Figure 22. Aphid infestation rate in plot 8.



Abundance=X/N2

Figure 23. Aphid abundance in plot 8 in 1993/1994.



Desity= X/N1

Figure 24. Aphid density in plot 8 in 1993 and 1994.

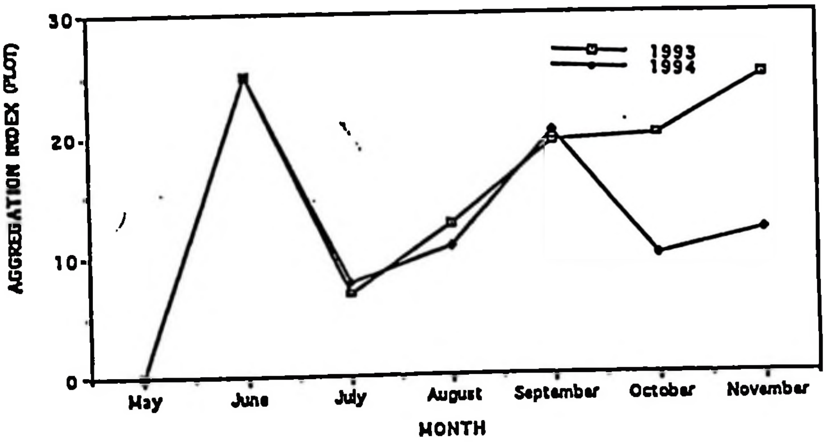


Figure 25. Aphid aggregation index inplot 8 in 1993 and 1994.

3.0 CHAPTER 3

LABORATORY AND FIELD EXPERIMENTS

3.1 Objectives

To study intra-tree dispersal of Cinara todocola, to determine at what stage and colony size do they abandon the colony which they have formed, to compare population growth in the laboratory, outside under shade and in the field (natural conditions) and to study the effects of aphids on host plants.

3.2 Materials and methods

Five healthy Sakhalin-fir plants were selected and planted into transplanting pots (one per plot). In early August a late 3rd instar nymph of C.todocola was inoculated onto the terminal shoot of each potted plant and on 6 branches of two, 10 year old Sakhalin-fir trees in the field of 1.8m ht. Three branches per tree were used.

Potted plants had 2 plastic cylinders placed around each plant (Figure 26). The smaller cylinder, 10cm in diameter and 20cm in height was smeared with adhesive (Kinryu -trade name) about 3cm wide at the base of the cylinder to trap emigrating aphids.

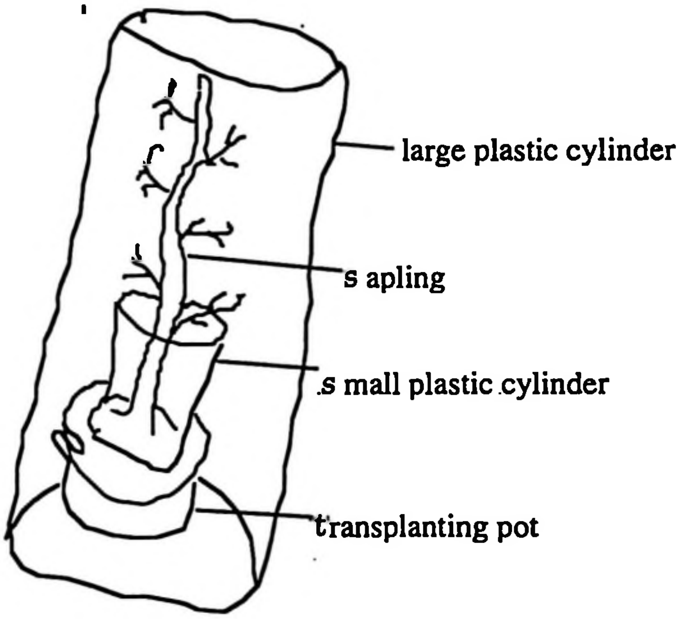


Figure 26. Potted sapling with two cylinders.

The larger cylinder was 27cm in diameter and 70cm height, and protected aphids from air currents. Three potted plants were kept in a controlled chamber: 15±1° C, 75-80%RH and 18:6 LD and the other 2 trees were left outside under the shade.

Some of the aphids released on the tree disappeared before they reached the adult stage or deposition of their progeny. On such trees or branches new nymphs were replaced again, and in some cases, this procedure needed further repetitions for realizing the settlement of aphids. Aphids were regarded as settled down when they were ascertained to cast their skins into the adult stage.

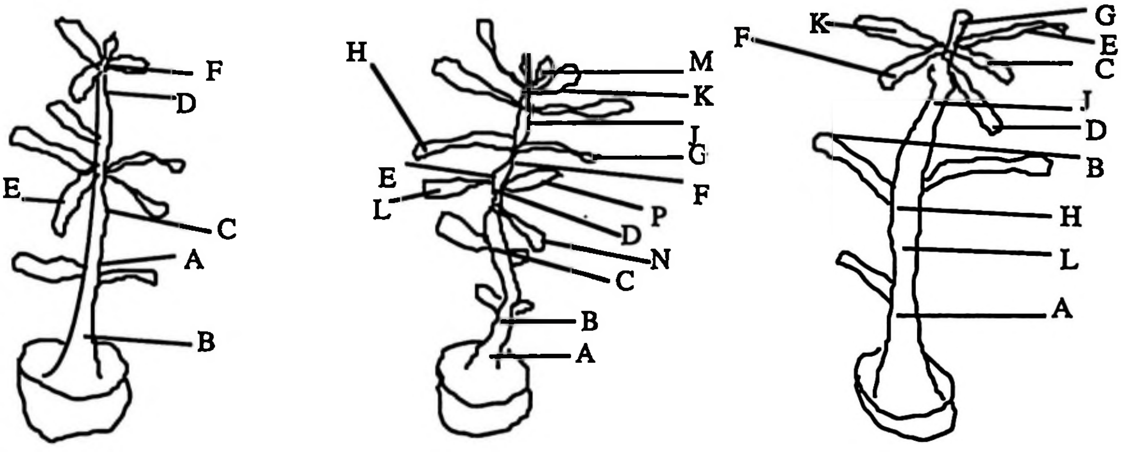
3.2.1 Data collection.

Aphids were counted without removal from the plants once per week from September through November. Number of aphids per colony, number of colonies per tree/branch, number of aphids trapped on the small cylinder, and tree condition and the movement of aphids within a tree were recorded .

3.3 Results

3.3.1 Controlled temperature

Although aphids were placed on a terminal part of the sapling, most settled along the stem, which indicates that they were looking for a suitable position. Position "A" was regarded as the point of initial settlement (Figure 27). Subsequent movement is denoted as "B", "C",---,etc. When inoculation was successful aphids started to reproduce (Figure 28). A settled aphid was regarded as a founder of a colony.



TREE NO. 1 TREE NO. 2 TREE NO.3

Figures 27. Position of aphids on a tree.

As reproduction started young aphids tended to stay with their mother, but later they began to move to new areas. Tables 15, 16 and 17 show numbers of aphids at different positions, numbers trapped, and tree condition. As new movement continued, aphid populations also increased and the population curve slanted upwards. (Figure 29).

Table 15. Laboratory population dynamics. Tree number 1 aphid dispersal and population growth.

Aphid location	August	September					October			November			
	25.Aug	9/1	9/8	9/15	9/22	29.Sep	10/6	10/13	10/20	10/27	11/3	11/10	17.Nov
A	4	8	8	2	1	1	–	2	–	–	3	19	24
B				1	–	–	2	–	–	–	19	20	20
C				5	4	1	–	–	–	–	3	4	18
D				1	5	9	14	96	120	250	103	110	142
E					1dead	4	3	–	–	–	1	1	
E									1	3	1	–	
Total number	4	6	8	9	10	15	19	98.	121	286	130	154	204
No. trapped							1		5	15	165	32	28

8/18_aphid settled.
10/6_slight resin,10/13-resin 1/2 tree, 10/20_resin3/4 tree,10/27_resi 5/8 tree, 11/3_ tree became week.

Table 16. Laboratory population dynamics, tree number 2 aphid dispersal and population growth.

Aphid location	August	September					October			November	
	25.Aug	9/1	9/8	9/15	9/22	29.Sep	10/6	10/13	10/20	10/27	3, nov.
A	4	11	1	10	2	47	64	2	20	15	
B			5	15	3	22	11	2	20	10	
C				20	6	73	44	8	81	49	
D					1	3	4		22	20	
E					5	11	15	2	17	3	
F					40	14	8	1	63	25	
G					10	23	25	3	54	49	
H					9	22	7	3	18	14	
J					5	31	75	5	70	15	
K					8	44	30	1	–	8	
L						3	18	2	81	96	
M						8	–		10	–	
N							9	1	18	17	
P									1	–	
Total number	4	11	6	45	99	301	310	30	476	321	dying
No. trapped			5		3		9	71	20	285	400

9/22_slight resin, 9/29_resin 1/2 tree, 10/6_ tree weak, 10/13_tree bad condition, 11/3_dying, 11/2C 20 died out.

Table 17. Laboratory population dynamics, tree number 3 dispersal and population growth.

Aphid location	August	September				October				November			
	25.Aug	9/1	9/8	9/15	9/22	29.Sep	10/6	10/13	10/20	10/27	11/3	11/10	17.Nov.
A	1	1	1	1	1	–	–	–	–	5	-	2	18
B		2	1	1	1	1	1	–	–	–	6	1	36
C				1	–	–	2	–	–	2	7	15	25
D						1	3	16	23	30	21	3	12
E						1	1	1	–	–	15	22	11
F						1	3	6	5	17	55	65	45
G						3	6	16	23	32	19	35	31
H						1	–	–	–	–	1	19	1
J							1	4	2	5	5	7	6
K							3	–	spider	–	4	5	15
L											8	7	-
Total number	1	3	2	3	2	8	20	43	53	91	141	181	225
No. trapped		1	–	1	–	–	3	8	10	–	5	21	

Resin started to drip from plants on September 22 (tree no. 2), October 6 (tree no. 1) and November 3 (tree no. 3). Half of the 3 trees started to drip resin when the population size was 98, 301, and 225 on plants 1,2,3 respectively. Spiders were found on tree no. 3. Population growth was fastest on tree no. 2, followed by tree number 1. On November 20 tree no.2 died. The death of this tree may have been caused by a high population, although plant susceptibility to attack may be another possibility. By producing resin plants were trying to use a defensive mechanism to counteract the effect of attack, but it was too late. Carrying capacity of tree number 2 was reached rather faster than the other trees. Dispersal of aphids on this tree may have been caused by the high population density and deterioration of host condition. Leaves of tree no. 3 turned yellowish earlier and the saturation density of the aphid population could not be reached. Extinction of the aphid population followed, as the population curve continued to slant upwards (Figure 28). Maximum population size was 286 and 475 on trees no. 1 and 2, respectively. When saturation density was reached population density started to decrease. Two population peaks were observed on trees no. 1 and 2 (Figure 28). It is thought that plant number 2 was more nutritious than plant 1 and that the population pattern of aphids at position E (plant 1) was stagnant. This could have been due to the fact that the founder of the colony disperse after producing the young ones.

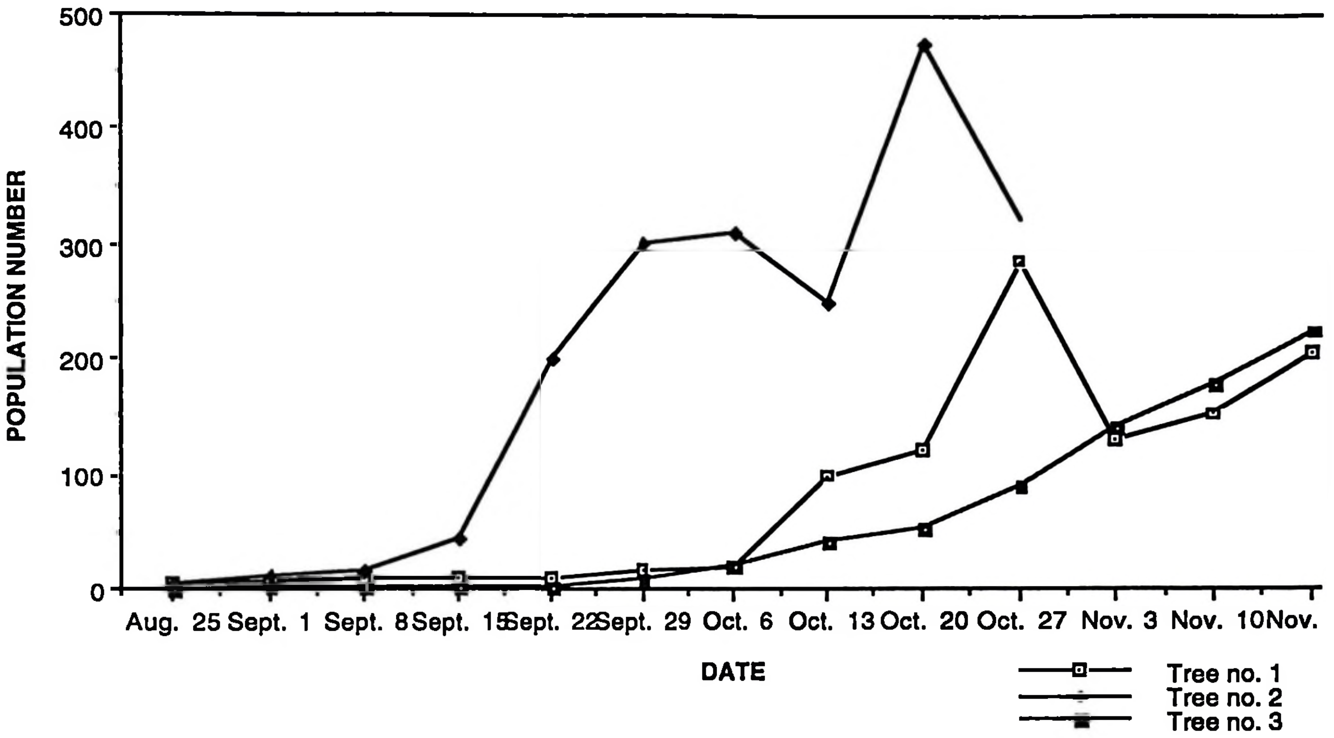


Figure 28. Laboratory population dynamics on 3 trees.

At the beginning aphids moved singly or in small numbers, but after this in larger numbers. After September dispersal was recorded at each point and the movement involved both adults and young insects, the 3rd instar nymphs in particular. Although all stages of aphids showed some movement, movement of adults may be caused by the need to locate suitable areas to deposit young. However, it is not clear as to why the 3rd instar nymph movement was so conspicuous. It is suggested that since winged aphids were not produced during the 2nd generation as reported by Yamaguchi (1976), the function of this instar is dispersal.

Population increase was observed for a second time after saturation point on trees no. 1 and 2 (Figure 28). This increase could have been caused by loss of aphids due to dispersal. Tree condition started to deteriorate and the curve started to bend downwards (upper asymptote). Many aphids started to abandon the plant and moved downwards along the trunk and most were trapped on the sticky band. Number of aphids trapped increased linearly and especially increased dramatically when population size became more than 300 aphids. Males were not observed in this experiment, probably due to the 18:6 L:D light conditions.

3.3.2 Trees left outside

Population growth of the saplings left outside under the shade was faster than those in the controlled chamber (Figure 29).

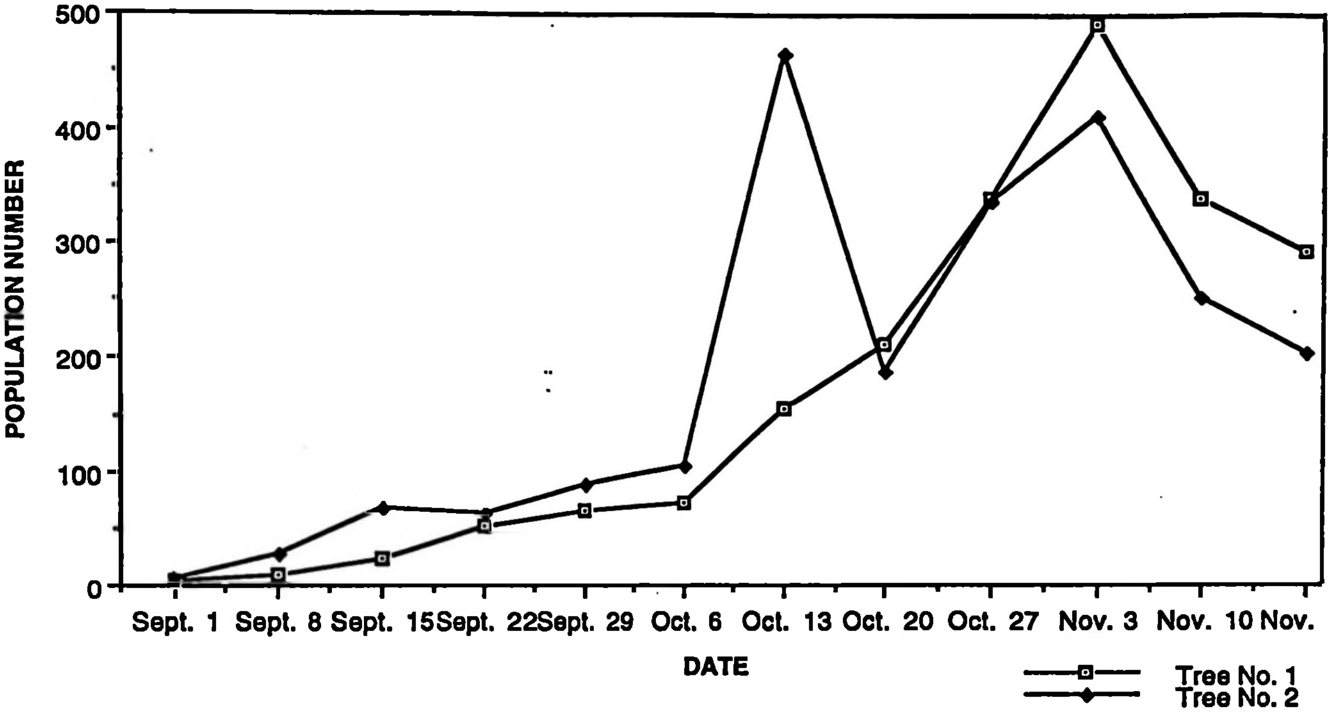


Figure 29. Population density of aphid on saplings left outside under the shade.

Also movement of the aphids started in large numbers earlier on these saplings than those in the chamber due to higher temperatures. Tables 18 and 19 show the number and movement of aphids to new areas, while Figure 30 shows position of aphids on the tree. "A" is the position where the founder established its colony and other letters indicate new invasion sites as above.

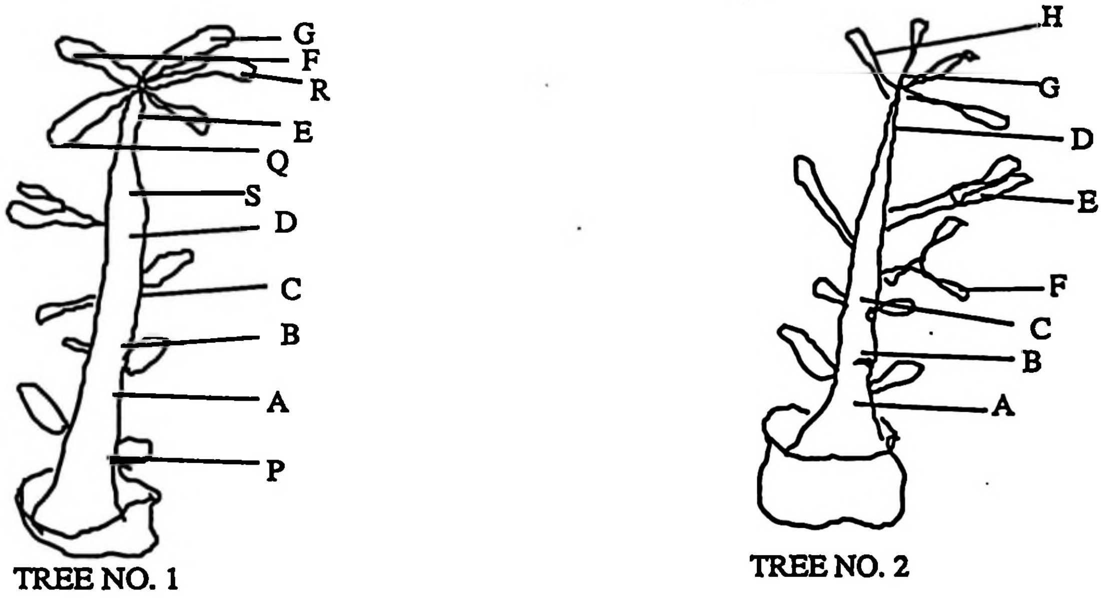


Figure 30. Position of aphids on saplings1 and 2 left outside under shade.

During dispersal most aphids moved towards the upper plant parts. The reason as to why aphids moved towards terminal shoots is probably the presence of young plant parts. Population growth was higher on tree no. 2 than on tree no. 1. Maximum population density was 493 aphids (tree no. 1) and 468 aphids (tree no. 2).

Table 18. Population dynamics of the saplings left out side under the shade, aphid dispersal and population growth of tree number 1.

Aphid location	DATES												
	August	September					October				November		
	25.Aug	9/1	9/8	9/15	9/22	29.Sep	10/6	10/13	10/20	10/27	11/3	11/10	17.Nov.
A	—	4	1	1	1	–	1	–	–	–	–	–	-
B			1	1	1	–	1	19	31	9	2	–	-
C			1	1	–	1	1 –	37	22	70	14	8	-
D			2	3	–	–	7	2	1	5	25	28	20
E			3	8	7	–	–	1	–	31	34	7	38
F			1	–	9	22	–	33	57	90	119	76	95
G			1	7	1	1	37	–	42	59	49	52	47
P			–	4	36	43	7	1	–	–	–	–	-
Q							1	53	42	56	130	70	50
R							20	10	17	19	47	32	34
S											73	67	8
Total number		4	10	24	54	67	74	156	212	339	493	340	292
No. trapped				2	8	2	–	14	10	26	211	18	

Number of immature males produced on each location

10/20-B-5, C-2; 10/27-B-2,C-7,D-1,E-4Q-8,F-20, G-7+1mummy, R-2; 11/3-E-4,Q-22,F-16,G-7, S-8, D-3,C-1;
11/7-E-4+2winged,Q-3+1winged,F-8+11winged,G-3,R-1+3winged.

Table 19. Population dynamics of the saplings left outside under the shade, aphid dispersal and population growth of tree No. 2.

Aphid location	DATES												
	August	September					October				November		
	25 Aug	9/1	9/8	9/15	9/22	29.Sep	10/6	10/13	10/20	10/27	11/3	11/10	17 Nov.
A	–	8	22	50	22	39	6	–	–	–	–	–	-
B			1	3	4	1	15	12	26	10	2	–	4
C			2	2	25	7	22	363	76	130	120	25	16
D			3	6	14	28	51	63	86	28	111	70	33
E			1	7	–	16	12	30	–	159	80	79	50
F										10	100	80	40
G												–	40
H													21
Total number		8	29	69	65	91	106	468	188	337	413	254	204
No. trapped					2	15	–	306	6	18	320	70	

Number of immature males produced per location

10/3- B-3,C-4,D-5,E-4; 10/20-8-10, 10/27-B-1,C-22,G-4,0-6,E-58; 11/3-D-22,E-10,G-30,C-3.

When maximum population size was attained population increase on both plants stopped and started to decrease (Figure 29). Due to high population growth there was a sudden increase in the movement of aphids in small, and then in large numbers into new areas. A second peak was observed on tree no. 1, this was probably caused by a slight recovery of the plant or through space created by the dispersal of aphids. This movement involved both adults and young insects.

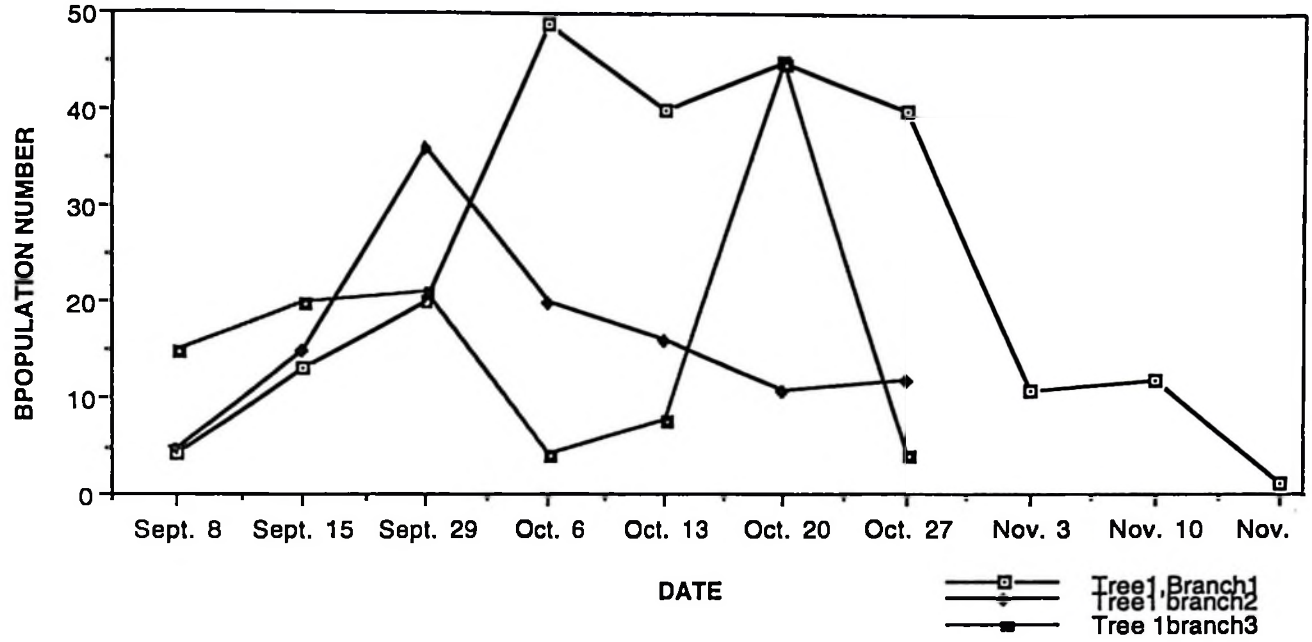
It is very difficult to estimate at what colony size aphids began to move, since movement was observed even in a small colony of 4 aphids. However, many aphids were trapped when population size exceeded more than 400 (Table 18 and 19), it is thus suggested that there must be some threshold for mass dispersal. The 3rd instar nymphs and matured adults were the most mobile insects. However, mass movement which involved all stages was observed when the colony was large. It was also noted that members of the colony started to move when disturbed by a dispersing aphid.

In this experiment exudation of resin was not observed. Male (winged) aphids were produced from October 3 on tree no. 2 and on October 20 on tree no. 1. Production of winged aphids could have been due to high temperature, food condition, or day length.

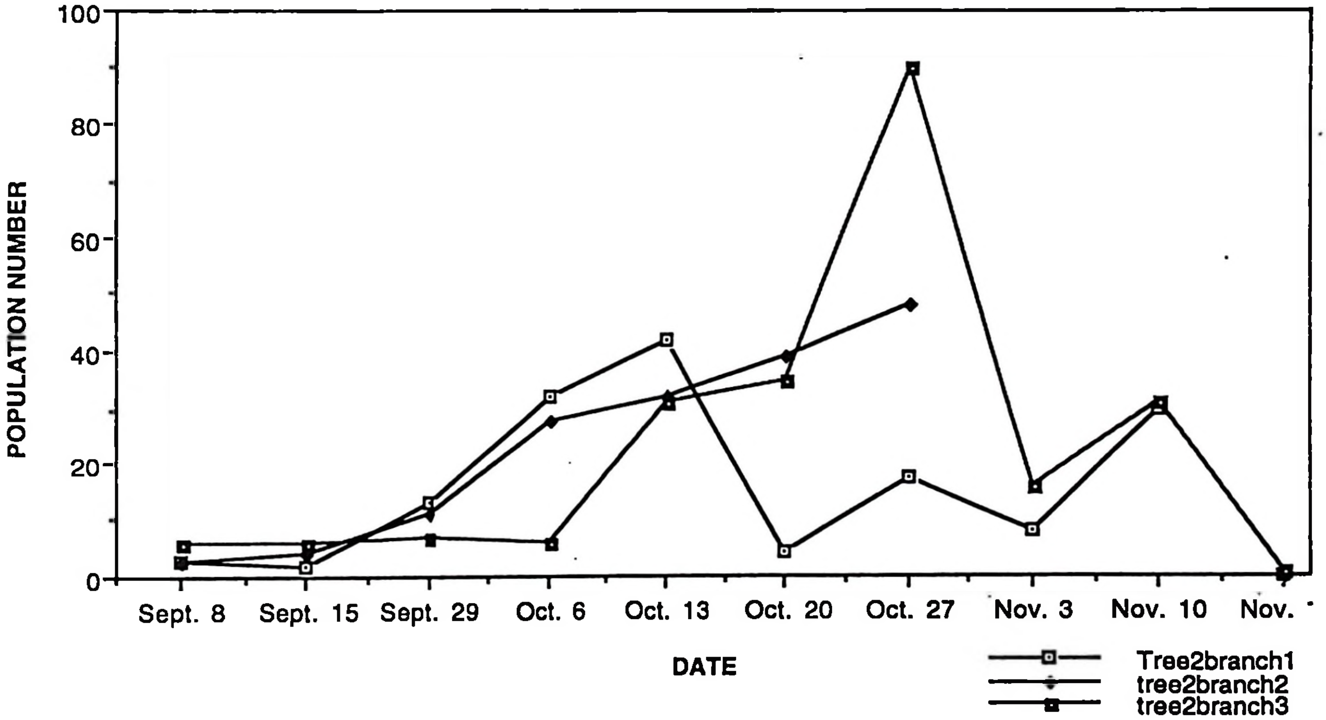
3.3.3 Field experiment

Population growth of aphids in the field was the lowest. This could have been due to environmental conditions and predation. Aphids settled very late in this experiment. Figure 31 shows aphid population growth in the field.

Tree No. 1



Tree No. 2



Figures 31 (tree1 above) and (tree 2 below). Population growth of aphids on field trees.

Table 20. shows the number of aphids and their position on a tree. Founders were first located at position "A", new movement to "B" and "C". Positions B and C are towards the apex (Figure 32) the plant was 10 years old, so the aphids migrated to the tips to feed on young plant parts. Population growth on both trees had 2 peaks except for branch no. 2. Branch no. 2 of tree no. 1 had 1 population

peak, while that of tree no. 2 did not reach saturation point.

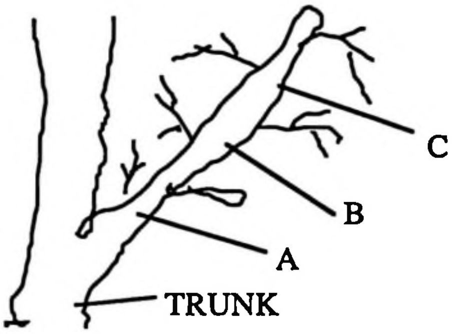


Figure 32. Aphid position on the field trees.

Table 20. Population dynamics of aphids on field trees, aphid dispersal and population growth on tree number 1 and 2.

Aphid location				DATES								
		September			October				November			
Tree number 1		9/1	9/ł	15.Sep	29.Sep	10/6	10/13	10/20	10/27	11/3	11/10	17.Nov.
Branch No. 1	A		4	13	10	35	40	45	40	11	12	1
	B		4	–	10	14	–	–	–	–	–	-
Total number			4	13	20	49	40	45	40	11	12	1
No. of immature males								8	7	1	1	-
Branch number 2	A		5	3	26	20	16	11	12	–	–	-
	B			9	10	–	–	–	–	–	–	-
	C			3	–	–	–	–	–	–	–	-
Total number			5	15	36	20	16	11	12	–	–	-
No. of immature males								1	1	–	–	-
Branch number 3	A		15	20	5	4	8	45	4	–	–	-
	B				16	–	–	–	–	–	–	-
Total number			15	20	21	4	8	45	4	–	-	-
Tree number 2 -												
Branch number 1	A		3	2	7	23	42	4	17	80	30	-
	B				6	9	–	–	–	–	–	-
Total number			3	2	13	32	42	4	17	80	30	-
No. of immature males									2	8	5	-
Branch number 2	A		3	4	11	28	32	39	48	spider	–	-
No. of immature males							2	6	7	–	–	-
Branch number 3	A		6	6	7	6	31	35	90	16	31	1 winged
No. of immature males							5	8	1	2	6	-

Therefore, tree condition was good and so dispersal could not have been caused by the deterioration of host plant condition. These aphids were attended by ants. Adults and the 3rd instar nymphs were the first to abandon the colony. Immature male aphids were observed on all branches from mid-October.

3.4 Number of males and colony size.

The number of winged aphids produced in a colony is thought to be related to colony size, deterioration of food quantity and quality. However, the production of male aphids started in October and ended in November. The number of males were identified during the immature stage by their conspicuous green colour and numbers related to total population size. The number of males increased with an increase in the colony size and vice versa. Table 21 shows the relationship between colony size and number of immature males produced in two saplings kept outside under shade, and six branches from two trees in the field. There was a significant correlation between the total number of males produced and colony size (F=120.7, df=10, P<0.001; Figure 33). A significant correlation was also observed when analysed separately (Figure 34). It is interesting to note that no males were produced on saplings kept under controlled conditions (15±1°C, 75-85%RH, 18:6 L:D). On the other hand the number of immature males produced per colony in 8 plots were also studied for 2 years. It was found that there was a weak but significant correlation between the number of immature males produced to the total number of individuals in the colony (F=95.75, df=127, P<0.001; figure b, page 18).

Table 21. Relationship between the number of immature C.todocola males produced to the colony size and date.

SAPLINGS				FIELD TREES			
Date	Immature males	Total number	percentage	Date	Immature males	Total no.	percentage
13.Oct	16	168	9.5	18.Oct	7	56	12.6
20.Oct	17	76	21.5	21.Oct	23	106	21.7
27.Oct	142	666	21.3	27.Oct	18	107	16.8
3.Nov	129	802	16.1	3.Nov	11	96	11.4
10.Nov	62	340	18.2	10.Nov	7	36	19.4
17.Nov	19	264	7.2				

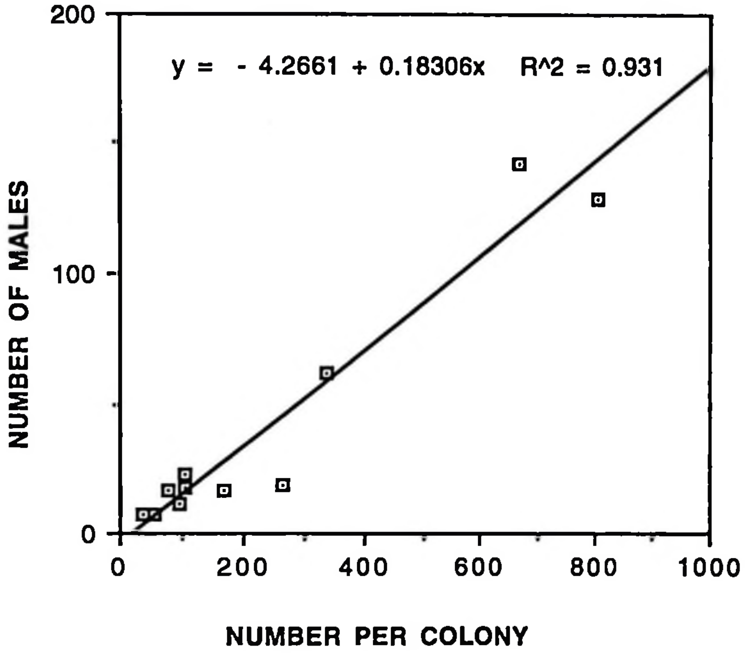


Figure 33. The relationship between number of males to colony size of <u>C.todocola</u>.

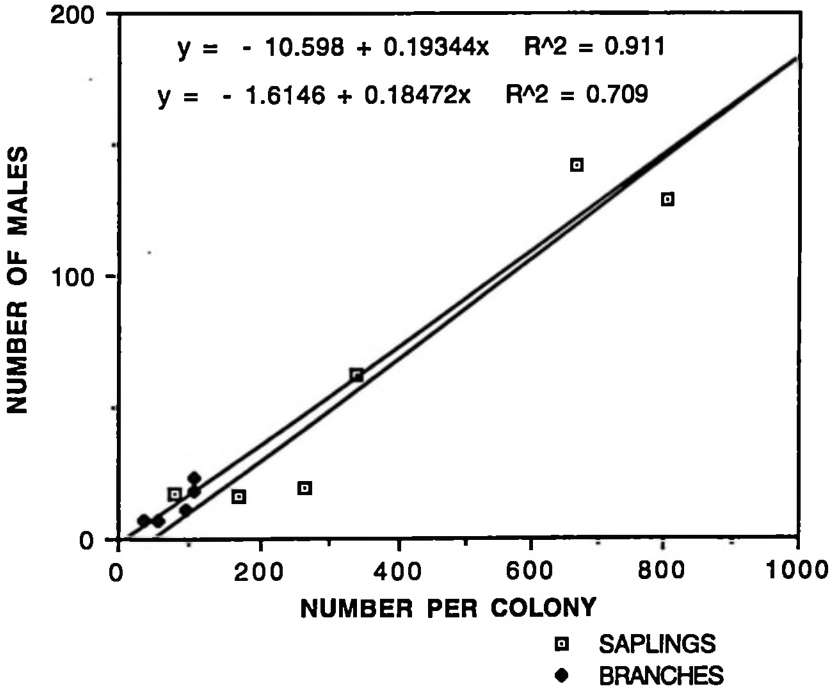


Figure 34. Relationship between the number of males to colony size on saplings and tree in the field. (Saplings- F=40.9, P=0.003. Branches - Not significant at P0.05)

4.0 CHAPTER 4

WALKING EXPERIMENT

4.1 Objective

Cinara todocola disperse by walking and in summer almost all stages move on the forest floor, although walking ability between stages differs. It is known generally that aphid movement activity increases with age, but it is not known if it is also the same for this aphid. This study was conducted to examine the effects of development stages, object sizes and colours on the walking distance of this aphid.

This experiment was divided into two parts. The first part was to investigate walking pattern, speed, maximum distance traveled by this aphid per unit of time and the effects of development stage on walking distance in a homogeneous environment. The second part was to study the effects of object sizes and different colours on aphid movement.

4.2 Materials and methods

a) A box made of plywood 1.8m length, 1.8m width and 1.8m height was used, and the inner part of the box was painted a white colour. This experiment was conducted at room temperature (21.5-23.0°C) at natural day lights.

Insects were released at the center of the box. Movement pattern and distance covered per 5 minutes interval were recorded (resting time included) for a maximum of 30 minutes. As an aphid walked its movement was traced with a white chalk. Insects were only allowed to walk on the horizontal surface, and termination of observation occurred when it started to climb the edges (vertical movement). Sampled insects were: stem mothers, 1st, 2nd, 3rd, 4th instars, viviparous and oviparous females of Cinara todocola were used.

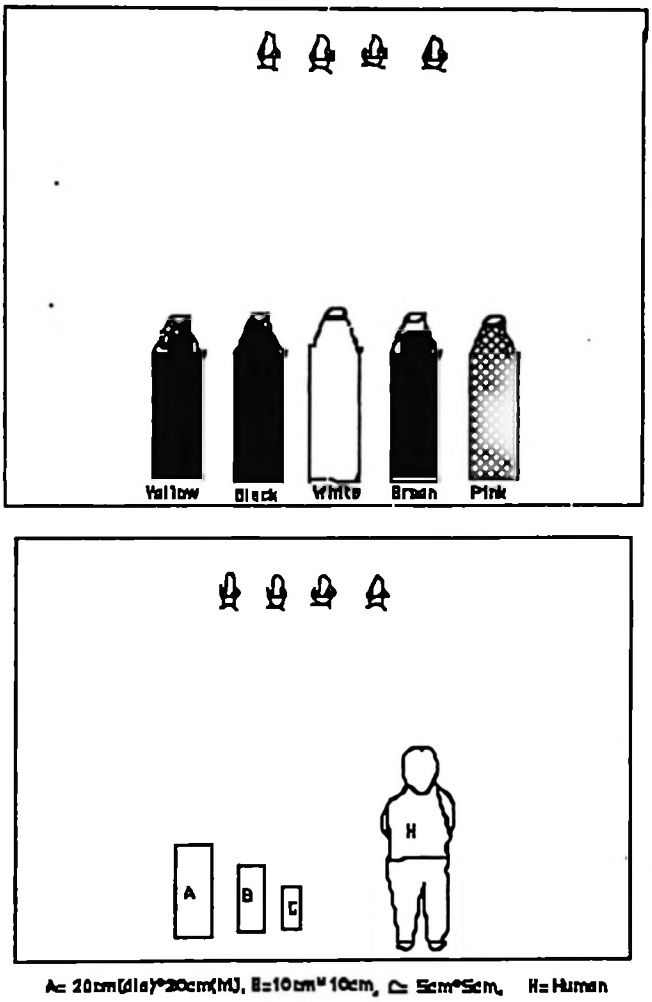
The following hypotheses were tested:

-That walking distance changes with time.

-That walking distance does not depend on the stage of the insect.

-Movement does not involve memory i.e. movement is random.

b) Four pieces of red pine (Pinus densiflora) logs of different sizes (20cm diameter 20cm height, 10cm dia. 10cm ht., 5cm dia. 5cm ht.), humans and 5 types of colours (1.5 liter plastic bottles were wrapped with paper ; green, yellow, pink, white, and black). Four 3rd instar nymphs were released one at a time on the box 75cm away from the object (Figure 35). Then number of aphids that reached the object, mean speed, and their path were recorded. Some insects like mosquitoes are attracted to thermal rays emitted by humans, so it was also an interesting study to see if this aphid is also attracted to humans.



1=Yellow

2=Black

3=White

4=Green

5=Pink

A=20cmht.,20cmdia.

B=10cmht.,10cmdia.

C=5cmht.,5 cmdia.

H=Human

Figure 35. Effects of different colours and object sizes on aphid movement.

4.3 Results

4.3.1 Walking

A total of 126 aphids were observed for 63 hours. About 756 movement events were recorded. There was no oriented approach towards the end of the box. Figure 36 shows a typical example of walking patterns of C. todocola. It was observed that 1st instar aphid walked around the release site. Other stages walked further distances and, when they reached the edge most of them turned back or went sideways and kept walking until they reached the opposite side. Some climbed up the edge.

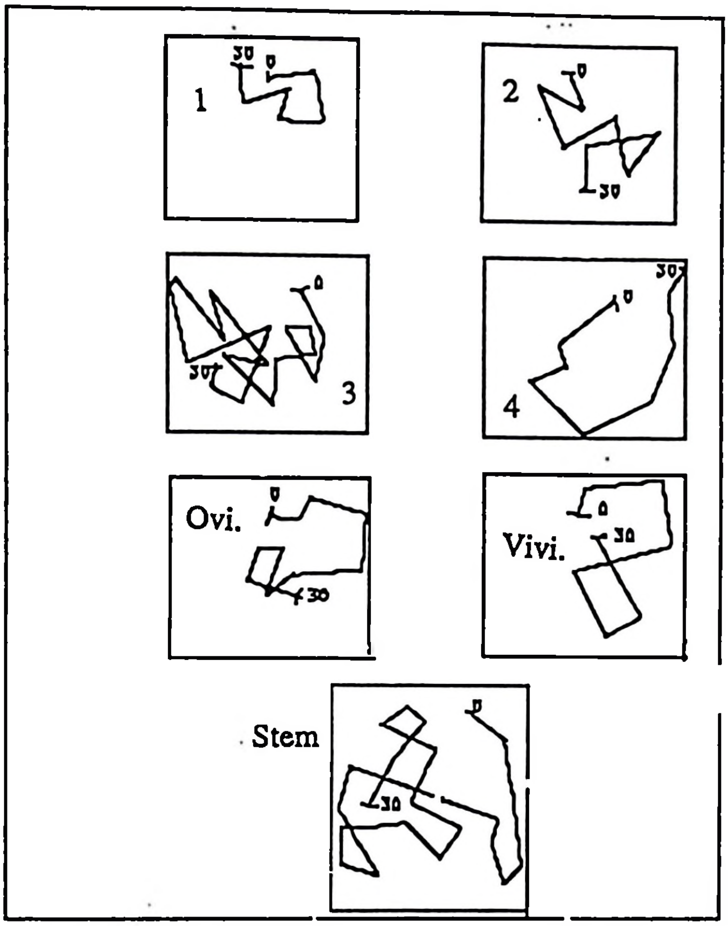


Figure 36. Diagrams of a typical paths of Cinara todocola in a wooden box (0-30) indicates minutes.

Total distance, Max-Min, and mean values are presented in table 22. It was found that 1st instar nymphs walked the least distance, while 3rd instars walked longer distances followed by the stem mothers (F=11.54, df=6, 35,P<0.001). Table 23 shows a Tukey multiple comparison matrix of pairwise comparison probabilities between stages.

Table 22. Total distance traveled per 30 minutes by different stages of C.todocoloa.

Stage/instar	Sample size	Min-Max (cm)	$\bar{X}\pm$SD (cm)
1st	7	105-259	178±46
2nd	28	112-581	302±127
3rd	37	135-734	383±155
4th	16	125-540	300±105
Viviparous	12	99-538	286±149
Oviparous	10	170-293	245±42
Stem mother	11	202-683	370±129

Table 23 Tukey multiple comparisons, matrix of pairwise comparisons probabilities.

Stages/Instars	1st	2nd	3rd	4th	Viviparous	Oviparous	Stem mother
1st	1						
2nd	0.0103	1					
3rd	0.0001	0.0366	1				
4th	0.0033	0.9995	0.0976	1			
Viviparous	0.01115	1	0.0332	0.9992	1		
Oviparous	0.0001	0.7741	0.0008	0.511	0.7956	1	
Stem mother	0.0027	0.1029	0.9993	0.2381	0.0944	0.0027	1

Significantly different when $P<0.0023$ (0.05/21tests)-Adjusted level of significance

Figure 37 shows average distance traveled by different stages of the aphid. It was observed that in all stages distances traveled between 5-10min. was greater than between 0-5min. thereafter, there was a tendency to decreasing distance with time except for the oviparous stages. Walking distance increased with development stage up to the 3rd instar nymphs then started to fall as observed in figure 37 (all stages).

The effects of stages and times on walking distances was analyzed using a 2 way ANOVA with stages and times as two factors. Significant differences were detected in both factors as seen in table 24a.

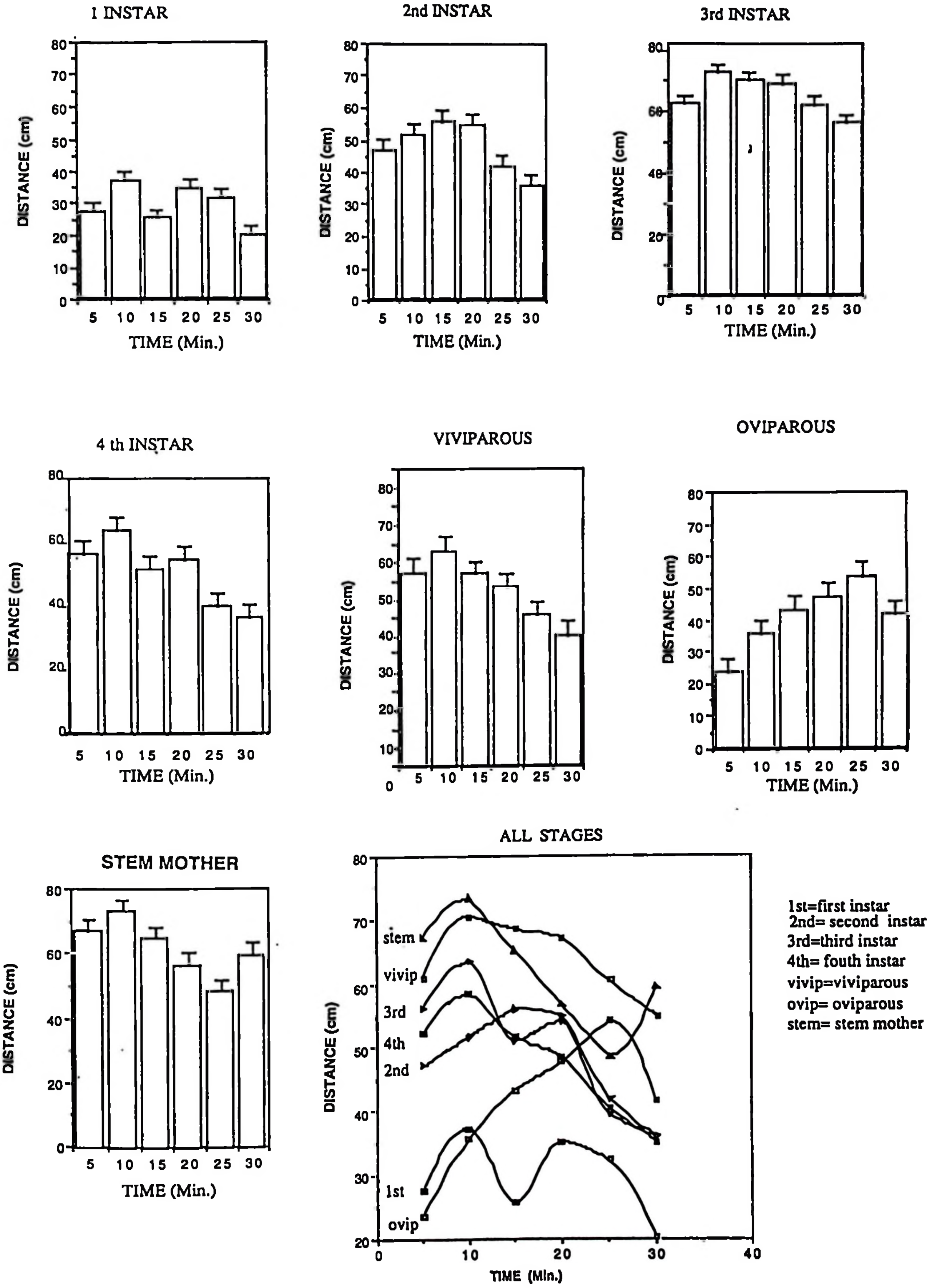


Figure 37. Mean distance traveled by C.todocola.

A multiple comparison test (Post-hoc test) was conducted to identify which combinations differ significantly. Table 24b shows a Tukey multiple comparison matrix of pairwise comparison probabilities for time and for stages (24c).

Table 24a. Two-way anova table on the effect of stage and time on distance traveled by C.todocola.

Source of var.	Sum of squares	df	Mean square	F_ ratio	P
Time	16440.02	5	3288	3.82	0.002
Stage	85521.85	6	14253.64	16.57	0.0001
TimexStage	25748.61	30	858.29	0.99	0.471
Error	6114103.85	714	860.06		

Table 24 (b). Tukey multiple comparisons,matrix of pairwise comparisons probabilities for time.

Time (min)	5	10	15	20	25	30
5	1					
10	0.039	1				
15	0.241	0.977	1			
20	0.326	0.945	1	1		
25	0.965	0.276	0.74	0.829	1	
30	0.66	0.005	0.056	0.087	0.711	1

==Significantly different if P<0.033 (0.05/15tests)

Table 24 (c). Tukey multiple comparisons,matrix of pairwise comparisons probabilities for stages.

Stages/Instars	1st	2nd	3rd	4th	Viviparous	Oviparous	Stem mother
1st	1						
2nd	0.005	1					
3rd	0.0001	0.0001	1				
4th	0.003	0.999	0.003	1			
Viviparous	0.024	1	0.001	0.999	1		
Oviparous	0.472	0.676	0.0001	0.482	0.833	1	
Stem mother	0.0001	0.0001	0.891	0.0001	0.0001	0.0001	1

==Significantly different if P<0.023 (0.05/21tests)

A regression method for analyzing animal movement pattern proposed by Inoue (1978) was used to describe the movement pattern of this aphid. C.todocola movement did not seem to involve memory because it exhibited a simple and general random movement (Figure 38). By plotting ln(1-F) against R^2 the line just passed through the origin and the slope was -1/Dt i.e. (w=0,p=0) thus, p is a linear function of t, which is the necessary condition for a process to be random (Broadbert and Kendal, 1953; Inoue, 1972). 1-F= is the proportion of vectors lying outside a circle of radius R, and R= distance traveled by aphids in cm. It can thus be said that C.todocola movement is random movement.

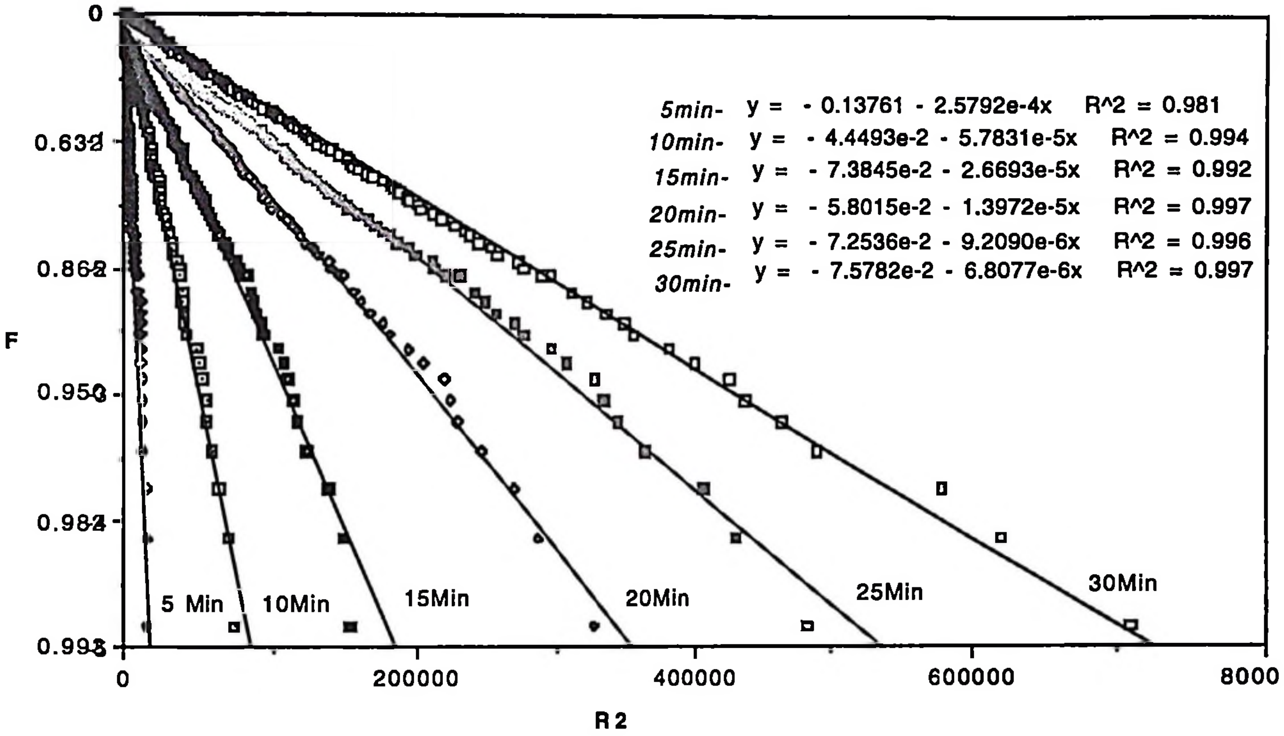


Figure 38. The relations of F and R in the general random walk process of C.todocola.

4.3.2 Colours and objects.

The number of 3rd instar nymphs attracted to the different colours and objects is shown in table 25 Speed per 5 minute towards the objects was also calculated.

Table 25. Number of aphids attracted to different colours, object sizes and average speed towards the object per 5 minutes.

	Yellow	Black	White	Green	Pink	Large	Medium	Small	Human
Aphid No.	15	1	0	20	5	19	7	2	30
Speed(X±SD)	-	-	-	-	-	145±15	125±19	115±40	130±17

X^2 (Chi-square) Colours X^2 =38.39, P<0.0001 Objects X^2 =32.62, P=0.001

Analysis of variance on speed to large object and humans was significantly different (F=9.68, df=1,47 and P=0.0032).

Typical aphid movement patterns towards the objects (Figure 39) was more or less similar as shown in figure 36, however, it is a bit directional.

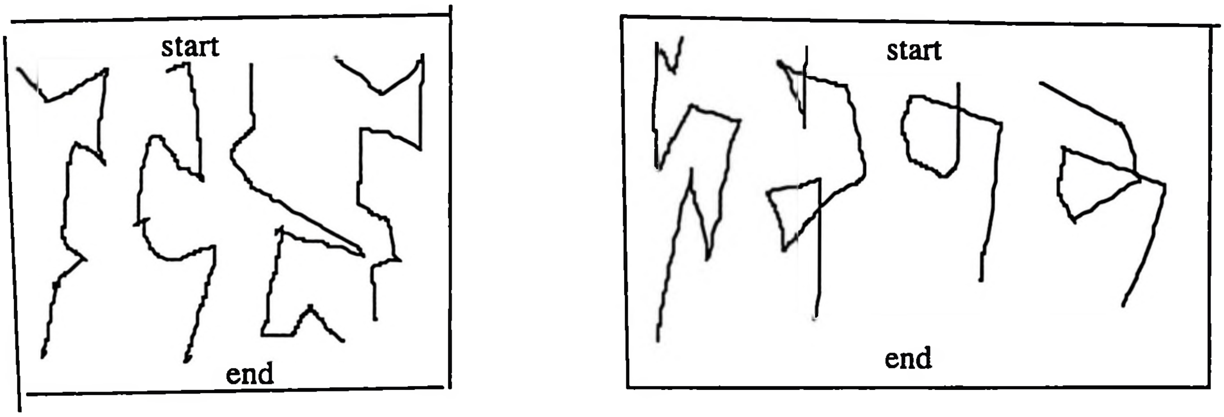


Figure 39. Typical movement pattern of the 3rd instar nymphs towards the objects.

Forty one aphids were used in colour and 58 aphids in object size trials. The following hypothesis was tested : equal number of aphids will be attracted to different colours and objects and each colour and object has an equal chance of being chosen. Chi-square was used to calculate if there was any significant difference among colours and object sizes.

The results showed that there was a highly significant difference among colours (P<0.00001, df=4) and object sizes (P<0.0001, df=3). Most of the aphids were attracted to green colour, while non visited white colour (Table 25). Large objects attracted many aphids than smaller ones . On the other hand human being attracted many aphids, however aphid's average speed was faster towards large object. A significant difference on speed towards human and large object was observed. It is difficult to explain as to why many aphids were attracted to human being because there are many factors that may have contributed, such as body size, shape, colour, thermal radiation, etc.

5.0 CHAPTER 5

WALKING SPEED ON DIFFERENT SURFACES

5.1 Objective.

To asses walking ability of aphid on different surfaces and to understand how different forest floor types may influence aphid walking speed.

5.2 Materials and methods.

The following surface types were used to study the effects of different surfaces on aphid movement: a wooden board, loose soft soil with about 50% moisture content, 50% compacted moist soil, fine sand with 1.5mm particle size (lighter than aphid body weight), coarse sand 3mm particle size (heavier than aphid body weight), and soil with vegetation (a piece of land 45cmX35cm collected from a forest with short and sparse grasses). Thirteen 3rd instar nymphs were released on each surface one at a time and left to walk for 5 minutes. Aphid movement was traced and horizontal distance measured. In the case of vegetation, a vertical distance was also recorded i.e. upward and downward movements along the grasses.

5.3 Results

Table 26 shows distance traveled by 3rd instar nymphs of C.todocola on different surface types for 5 minutes. It was found that insects had difficulties in walking on fine sand and soft soil because the particles were lighter than their body. When aphids grabed a particle it either fell down while carrying it or rolled with it. Grasses were found to obstruct aphid movement. When an aphid reaches the base of a plant some climbed up and down. There was a significant difference in distance traveled among walking surface types (F=37.4, df=90, P<0.001). Maximum speed was observed on the wooden board.

5.3.1 Distance traveled and body weight

The influence of body weight of C.todocola on its movement is not well known. To asses the effects of body weight of a stage on distance traveled, 3 stages of C.todocola that walked the longest distances in 30 minutes were used (stem mothers, viviparous adults and 3rd instar nymphs). Aphids were released on a wooden board one at a time. Their walking path was traced for 30min. and distance measured using a string. There was a significant correlation between body weight and distance traveled in stem mothers (F=81.74, df=14, p<0.001, R^2=0.82) and 3rd instar nymphs (F=6.51, df=14, P<0.023, R^2=0.31). However, no significant correlation was observed in the viviparous adult as seen in figure 40. Based on the above data, an analysis of covariance (ANCOVA) was conducted between stem mother and the 3rd instar nymphs to see the difference in level between the two regressions.

Table 26. Distance traveled by *C.todocola* on different surface types for 5 minutes.

Surface types	No. of aphids	min-max (cm)	X±SD (cm)
Fine sand	13	2-8	4.23±2.01
Soft soil	13	2-14	5.38±3.07
Vegetation	13		
_horizontal		2-20	6.77±4.57
Total		10-23	16.61±3.48
Compacted soil	13	42-59	49.23±5.07
Coarse sand	13	40-70	52.15±8.07
Wooden board	13	29-125	73.46±29.27

A two stage analysis was done, first was to be sure that there was no significant interaction between the covariant (stage) and weight (i.e. homogeneity of the slopes). Table 27a shows the probability value for the age by weight interaction is 0.372. Therefore, the assumption of homogeneity is proven. Analysis of covariance was then done and it was found that there was a significant difference between the two stages as can be seen in table 27b. This means that 3rd instar nymphs traveled a longer distance than stem mothers with the same weight (Figure 40).

In summer aphids were found to be restless and most aphid movements occurred during this period. To determine if temperature had any influence on aphid movement, 3rd instar nymphs were used with two temperature regimes (11°C and 25°C) to study the effect of temperature on aphid movements.

Third instar nymphs were released on a wooden board one at a time and their movements traced by using white chalk for a period of 30 minutes per nymph. Eight aphids were used in the 11°C and 37 aphids in the 25°C treatments respectively. It was found that temperature had an effect on aphid movement distance, however, the difference was not significant at the P=0.05 level (table 28).

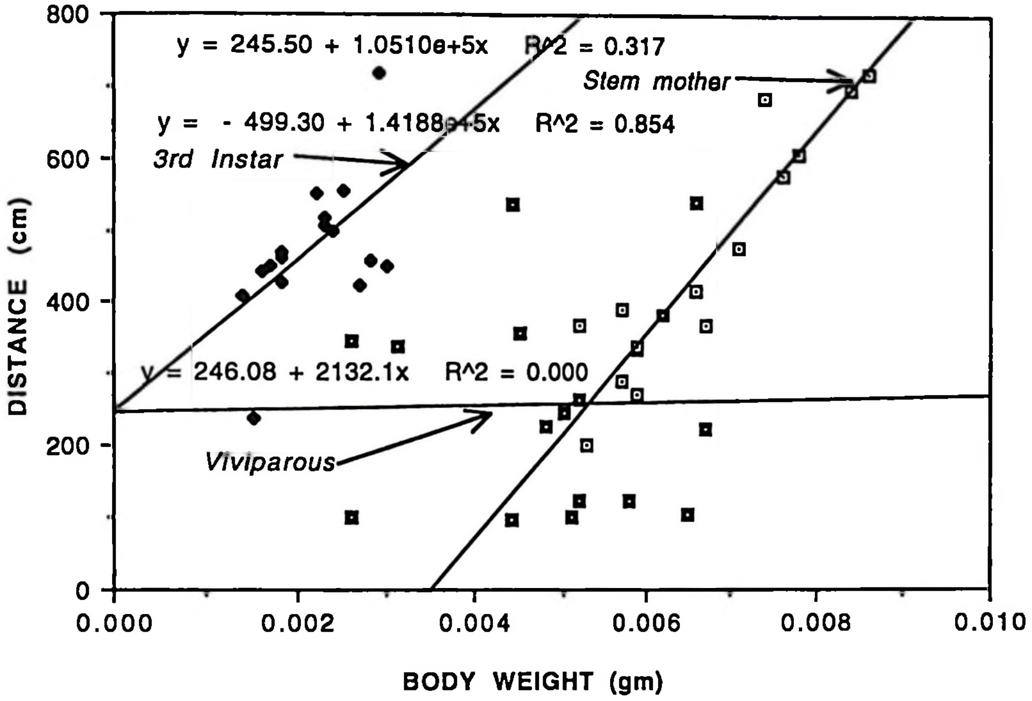


Figure 40. Relationship between body weight and distance traveled by 3 stages of C.todocola.

Table 27a . Analysis of variance on the homogeneity of the regression, distance and temperature.

Source of var.	Sum of squares	df	Mean square	P
Treatment(age)	149694.92	1	149694.92	0.0001
Covarite (weight)	203831.27	1	203831.27	0.0001
Age X Weight	4664.51	1	4664.51	0.372
Error	158647.85	28	5665.99	

27(b)

Source of var.	Sum of squares	df		Mean square	P
Treatment(age)	393210.76	1	1	393210.76	0.0001
Covarite(weig	399095.58	1	1	399095.58	0.0001
Error	163312.36	29	29		

Table 28. Effects of temperatures on the movement of the <u>C.todocola</u> 3rd instar nymphs.

Temp. °C	Aphid number	Min-max (cm)	X±SD (cm)
11	8	147-486	346±99.85
25	37	175-551	441±114.3

6.0 CHAPTER 6

COMPARISONS OF C.TODOCOLA AND OTHER APHID SPECIES

6.1 Objective.

Although most aphids disperse by flight, intra-tree movement is more/less done by walking. There are many species of aphids that are found close to the soil surface e.g. herbaceous and agricultural crop aphid species. It is assumed that these aphids may have developed walking ability like C.todocola. The following experiment was conducted to compare the walking ability of C.todocola with tall tree-, herbaceous- and agricultural aphid species. Also the effect of weight and two temperature treatments (11°C and 25°C) on distance traveled was examined. Selection stages of other species for comparison with the C.todocola 3rd instar was based on an initial trial which compared walking ability of different stages and the stage which walked longest distance in 30 minutes was selected.

6.2 Materials and methods

Third instar nymphs of C.todocola were compared with the adult maple aphid- Periphyllus californiensis (tall tree), the benibana aphid- Acyrthosiphon solani and karasuno-endo aphid- Megoura crassicauda (herbaceous) and momoaka aphid - Myzus persicae (agricultural -on radish). Aphids were released on a flat wooden board one at a time at room temperature conditions, and left to walk for 30 minutes while tracing their path. Aphid body weight was taken after each observation. The second part of the experiment involved releasing aphids on the board at one of two temperature treatments, and comparing distances moved by each species.

6.3 Results

Mean body weight of Cinara todocola, momoaka and benibera aphids were more or less the same but C.todocola moved longer distances (Table 29).

Table 29. Comparison between C.todocola and 4 different aphid species on weight and distance traveled.

Species	n	WEIGHT $\bar{X}$±SD (g)	DISTANCE $\bar{X}$±SD (cm)
C.todocola	16	0.002±0.0005	473.43±97.46
Maple aphid	16	0.0011±0.0004	79.56±33.35
Benibanaaphid	16	0.0024±0.0007	390.44±101.56
Karasuno endo aphid	16	0.0014±0.0001	270.43±65.7
Momo aka aphid	16	0.0021±0.0004	252.19±61.63

Relationship between distance traveled and weight of C.todocola with 4 aphid species was compared as shown in Figure 41. The regression slopes of C.todocola, momoaka and maple aphids were found to be a bit parallel. Analysis of covariance (Ancova) was done to test the homogeneity of the slopes. The first step was to be sure that there was no significant interaction between the covariate (species) and treatment (Weight). Table 30 shows that the probability value for the treatment by covariate interaction was 0.1723 in a two-way analysis of variance on the effects of species and weight on the distance traveled, an ad-hoc test was conducted to examine which species differed significantly .

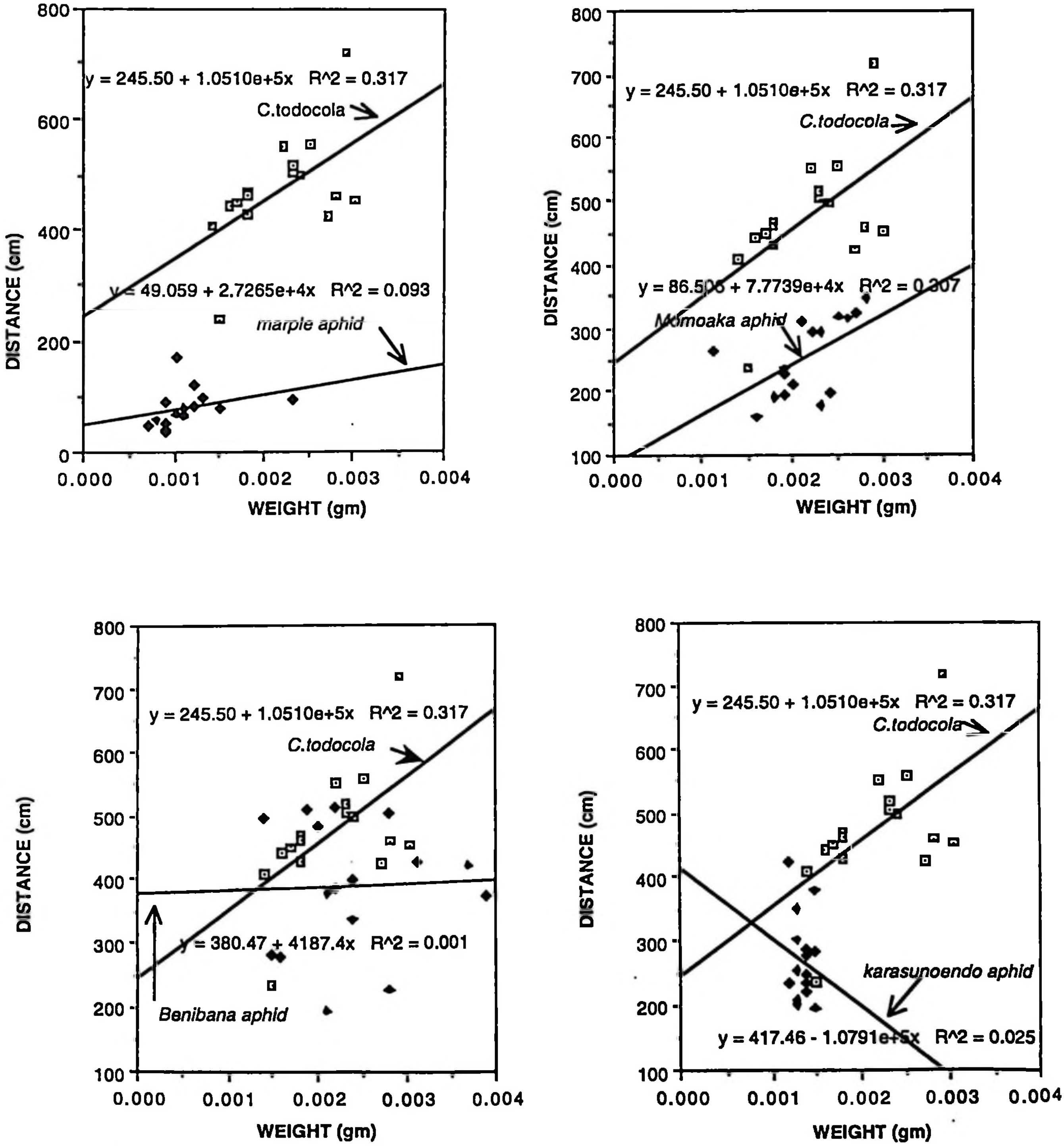


Figure 41.Relationship between body weight and distance traveled by C.todocola and four different species of aphids.

Table 30. Two way analysis of variance of the effects of species and weight on the distance traveled by different species of aphids.

Source of var.	Sum of squares	df	Mean square	F_ratio	P
Species	88979.97	4	22244.99	4.213	0.0041
Weight	1336.26	1	1336.26	0.253	0.6165
Speciesxweight	34776.06	4	8694.01	1.6467	0.1723
Error	369585.38	70	5279.79		

Source of var.	Sum of squares	df	Mean square	F_ratio	P
Species	797194.55	4	199298.64	36.47	0.00001
Weight	31230.75	1	31230.75	5.71	0.0194
error	404361.44	74	5464.34		

Tukey multiple comparisons, matrix of pairwise comparison probabilities on species.

Species	C.todocola	Maple aphid	Benibana aphid	Karasunoendo	Momoakaaphid
C.todocola	1				
Ma ple aphid	0.0001	1			
Benibana aphid	0.0001	0.0001	1		
Karasunoendo	0.0073	0.0001	0.1272	1	
Momoakaaphid	0.0001	0.0021	0.4216	0.0002	1

==Significantly different if P<0.05

As seen in figure 41, for a given weight of aphid it was found that C.todocola walked a longer distance than momoaka and maple aphids. It is thought that, at weights below 1.3mg (benibana) and 0.9mg (karasuno-endo) C.todocola walked a shorter distance, which indicates that with an increase in weight there is a decrease in distance traveled by benibana and karasuno-endo aphids.

Temperature had a significant effect on aphid movement in the three species, C.todocola, maple and benibana aphids. Table 31 shows that at the lower temperature all species of aphid moved shorter distances. At 11°C C.todocola moved a longer mean distance than other species. However, at 25°C momoaka aphid moved a longer distance than C.todocola. A two way analysis of variance was used to compare <u>C.todocola</u> with maple and karasuno-endo aphids, there was a significant difference in both species (F=73.72, df=2 and P<0.0001) and temperature (F=10.55, df=1 and P=0.0015).

Table 31. Comparison between <u>C.todocola</u> and different aphid species of the effect of temperature on distance traveled.

	TEMPERATURE			
		11°C		25°C
Species	n	$\bar{X}$±SD (g)	n	$\bar{X}$±SD (cm)
<u>C.todocola</u>	8	346.13±99.86	37	382.62±155.30
Maple aphid	10	195.30±46.72	20	275.50±62.99
Banibanaaphid	28	76.89±26.58	33	141.24±37.67
Karasuno endo	–	–	15	256.07±61.74
Momo aka aphid	–	–	16	390.44±101.56

In the nalysis of variance on the effects of temperatures on distance traveled by 5 different species of aphids there was no significant diference in the interaction factor, however a highly significant difference were observed between species and temperatures (species- F=73.7,df=2,130,P<0.001; temp.=F=10.4, df=1,130, P=0.0014).

7.0 CHAPTER 7

DAILY DISPERSAL PATTERN

7.1 Objective.

In summer aphids were found to be in constant motion, and individual movement was more frequent than mass movement. To understand at what time of the day mass movement occurs the following experiment was conducted.

7.2 Materials and methods.

Two healthy Sakhalin-fir saplings (70 cm ht) with different numbers of aphids were used, one tree per day. Tree A had 236 aphids in 21 colonies and tree B 24 aphids in 6 colonies. The position of each aphid, its colony, and the number of aphids on the sapling were recorded. This experiment was done over 2 days at room temperature. Data recording was done at intervals of 1hr from 8:00 a.m to midnight, and at 3 hour intervals from midnight to 8:00 a.m. Aphid movement was recorded when an aphid moved 5cm from its previous position. From 18hrs evening room lights were switched off, and observation was done using a reading light. At the base of the sapling a layer of sticky substance was smeared (Kinryu-trade name) to trap dispersing aphids.

7.3 Results.

Mass movement was observed between 10-11hrs (28°C) and 12-13hrs(29°C) on tree A, and 10-11hrs and 17-18hrs (26°C) on tree B. Dispersal trends for two days on the two trees were more or less similar as shown in figure 42.

After 19hrs no aphid movement was observed. It can be said that this aphid disperses during day light hours and movement is also influenced by temperature.

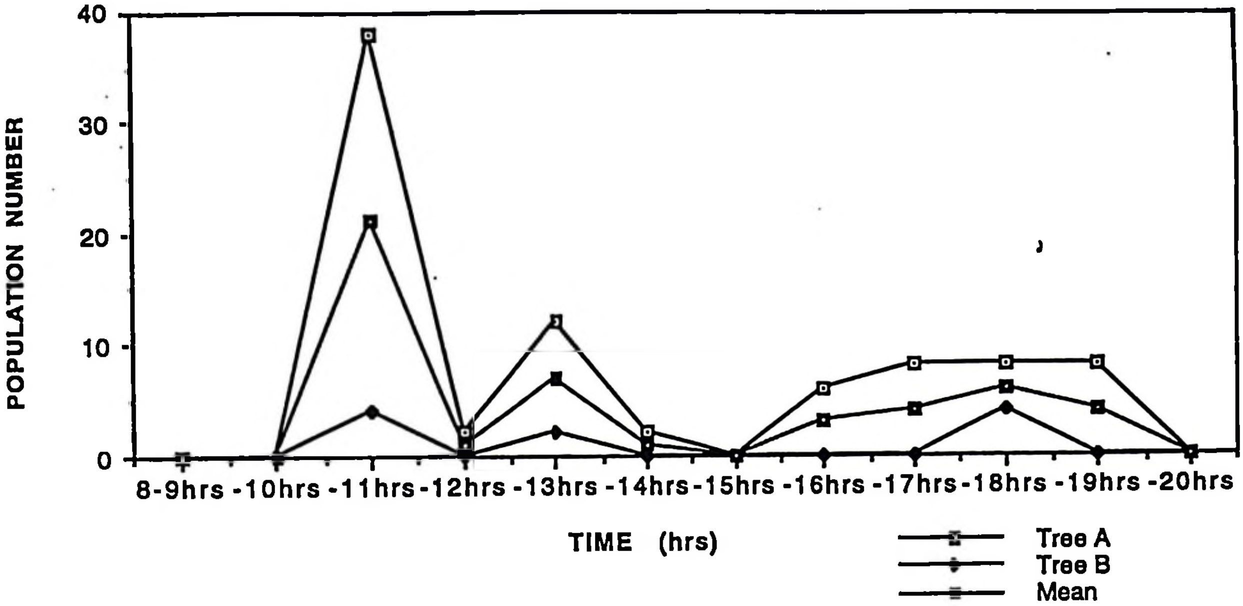


Figure 42. Daily dispersal pattern of C.todocola.

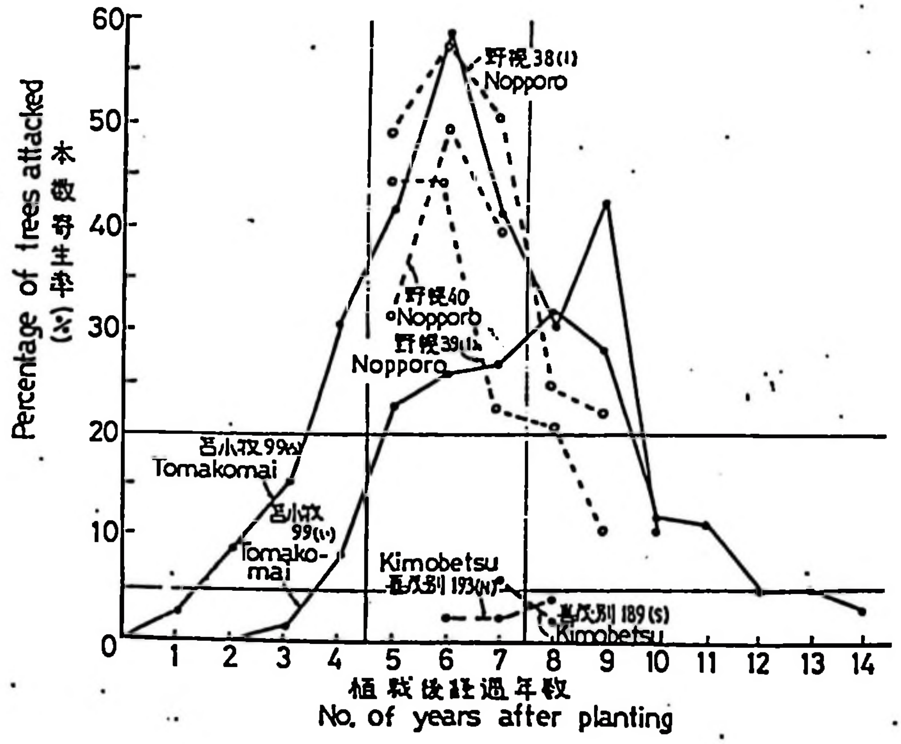


Figure 43. The effect of plant age on aphid population (Yamaguchi,1976).

8.0 CHAPTER 8

DISCUSSION

8.1 DISPERSAL

Cinara todocola aphids at all stages of development move about over the surface of their host plants and even between adjacent trees. This movement resulted in slow diffusion dispersal. The 3rd instar was more highly mobile than other stages. Yamaguchi (1976) argued that the movement of apterae of Cinara todocola seems to be based on an innate locomotive behaviour and is accelerated by extrinsic factors such as deterioration of host trees or high densities. This argument is not very different from Johnson et al. (1969) who reported that the tendency to disperse is an evolved adaptation that has enabled aphids to spread the chance of survival in space and seek out and colonize plants that are above average quality. In this experiment the movement of the 3rd instar nymphs, both viviparous, and oviparous may be related to this adaptation since their movement was sometimes density-independent. Viviparous and oviparous movement was due to trying to locate a suitable site for reproduction but the reason for 3rd instar's was not established. It is thought that since alates were not produced in the 2nd generation, this morphs function is dispersal. It is assumed that although crowding markedly influences the readiness with which viviparous and oviparous aphids disperse in the 3rd instar, a crowding stimulus was not required. In these experiments, crowding, host plant condition, presence of natural enemies and brushing by migratory individuals caused dispersal.

8.1.1 Crowding.

Most authors agree that crowding may cause dispersal but have failed to mention the minimum number of individuals in a colony or on a tree that will trigger dispersal. This could be due to the fact that there are many factors that may induce aphids to disperse. In the present study aphids were found to disperse even when population size was only four. It was proposed in chapter 3 that there must be a threshold number of aphids in a colony or a plant that will trigger aphid dispersal. However, crowding is not the only factor that causes dispersal. Interaction of these factors may also complicate this. Crowding during nymphal and adult early life will encourage the production of dispersing aphids (Johnson,1969; Shaw,1970bc; Dixon et al.,1968; Walters and Dixon,1982). Despite high population densities aphids on trees in open area plots did not disperse into adjacent trees. They remained on the plants until they all died. It is assumed that aphids assessed that the risk of dispersing was higher than staying on a deteriorating plant. Although dispersal results in the colonization of suitable plants, Dixon (1969) pointed out that it is not always clear what advantages there in dispersing except from annual plants that are about to die. This is true since dispersal can be costly in terms of fecundity or survival or both. Burns (1971) reported that by dispersing potential fecundity is reduced and produces a delay in the onset of reproduction, the combined effect of which is a marked reduction in reproductive potential and rate of increase. In addition to the assumed high mortality rate that will be suffered during dispersal, aphids tried to delay departure until the host quality fell below the average expectation, by which time it may be too late as was observed in those plots under direct sunlight. It is not clear as to why those aphids decided to remain on a tree until they all died. When host condition deteriorates there are advantages to an aphid in investing more resources in locomotion and dispersing to other host and less into reproduction (Mercer, 1979).

8.1.2 Nutrition.

Plants differ in nutrient quality both within and between seasons, therefore, the degree of differential dispersal shown by aphids probably reflected both the within and between year heterogeneity of the environment. Dispersal rate in 1994 was higher than in 1993. This was probably caused by higher population growth in 1994 and high temperatures. However, the distribution of aphids between and on the host plant may be caused by variations in the quality of phloem sap. At the beginning of the population growth there was no tendency for the aphids to prefer a particular part in the plant although most settled near the top part of the plant. Kennedy et al. (1950) and Ibbotson and Kennedy (1950) reported that not all parts of a plant are an equally suitable source of food for aphids, they tend to move more frequently when feeding on a poor rather than a good food source. This results in aphids colonizing parts of plants on which they can achieve the highest growth and developmental rates. In turn this will result in high population density and cause population pressure, which will lead some aphids to disperse.

Whitham (1978) when studying leaf selection in galling aphid (Pempigus batae) showed that the best feeding sites are limited. When two stem mothers attempt to settle on the same leaf, a kicking and shoving contest follows that can last for two days. The larger aphid usually wins, displacing the loser to a more distal position along the midrib. Generally leaves grow faster at the base than at the tip. By means of territorial behaviour, large aphids can deny other individual's access to the best leaves. Fight for space was also reported by Aoki and Makino (1982), when working with Epipiemphis niisimae. An individual's exact location often determines its fitness. It was found that aphids may visit and immediately leave the plant and this could be due to poor quality of phloem sap. An aphid is said to sense the suitability of a plant within 60 seconds without stylet penetration (Harris, 1977; Pollard, 1977). Once an aphid settles it probes deeply into the plant. During superficial probing an aphid imbibes a small amount of plant sap (Mac lean and Kinsey 1968; Shambaugh et al., 1978; Bromley et al., 1979, 1980; Bromley and Anderson, 1982 ; Tarn and Adams, 1982 and Tjallingi, 1978). Aphids are likely to settle on a good rather than poor quality host (Walters and Dixon, 1982). If an aphid settles on a poor quality host the settling response is quickly inhibited and they leave the plant. The above statement is also supported by Walters and Dixon (1984) who reported that host quality affects the readiness to take off, and aphids generally depart sooner from poor-quality hosts and the shorter they stay the fewer off spring they are likely to leave behind. Kennedy and Booth (1951) proposed that host selection by summer generations of the polyphagus black bean aphid (Aphis fabae) was in response to nutrient quality and that the aphid returned to the primary host in autumn more in response to secondary plant substances (e.g. flavour) rather than nutrient quality. This was supported by Dixon (1971e) and Dewar (1977). However Hashimoto and Furuta (1988) reported that migration of alates in the second generation of maple aphid to late budding trees was considered as an efficient mechanism to secure food.

Klingauf (1971) found that the glucoside phlorizin, present in the leaves of apple and other pomoideae, promotes colonization by apple and other aphids Aphis pomi and Rhopalosiphum insertum. Similarly sinigrin, a characteristic of cruciferae, induces the cabbage aphid Brevicoryne brassicae to settle and feed (Wensler, 1962; Nault and Styer, 1972). Herger (1975) reported that rutin and quercetin have the same effect on the dock aphid (Aphis rumis). These substances often act as barriers to the colonization of plants by many aphids, but enable host specific aphids to recognize their host plants. Kloft (1977) suggested that the phloem sap of some resistant and non-host species is nutritionally unstable.

Wensler (1962) found that the cabbage aphid Brevicoryne brassicae will not settle and feed on plants lacking sinigrin but can be reared on leaves of broad bean provided they are impregnated with sinigrin. However, sinigrin has a negative effect on the growth of the polyphagus aphid Myzus persicae (Van Emden, 1972). High concentration of the flavonoids catechin and epicatechin in the late buds and flowers of rose are also thought to deter the rose aphid (Macrosiphum rosae) from feeding on these structures (Miles, 1978). The broom aphid Aphis cytisorum prefers to feed on the flowering stems of broom, which contains morquinolizidine alkaloids, rather than other parts of the plant that have a below average alkaloid content (Wink et al., 1979). However, what promotes colonisation and settling by C.todocola is not clearly known.

8.1.3 Host quality.

Deterioration of host plant was found to influence dispersal of C.todocola. In experiment two (chapter 3) aphids dispersed when the plant leaves started to turn yellowish, and in the laboratory experiment exudation of resin from host plants influenced mass movement of aphids. Dixon (1971c) reported that aphids leave quickly if the host quality is poor, but if quality remained above the average expectation, they either deposit young ones before dispersing or stay. The emigrants and sexuals of host alternating aphids are produced in anticipation of an inevitable deterioration in host quality. The morphs are obligate migrants and colonize other more suitable hosts. It is thought that it is an adaptive feature for individuals to leave when host quality is still above average expectation because it serves to increase the chance of survival by dispersing members of a clone in space.

8.1.4 Natural enemies.

It was observed that presence of a natural enemy (syrphid larvae) influenced dispersal of C.todocola. However, Dixon (1985) reported that in host alternative aphid species this has attracted little attention, since it was thought that host alternation, is a means by which some aphids escape their natural enemies. On the other hand Dixon (1971a) observed that when a large aphid population has developed on a primary host some of the winged (emigrants) escape from the natural enemies by moving to the other, secondary host plants. The new colonies, because of their isolation grow quickly. Therefore, movement from plant to plant would enable the aphid to exploit the spatial heterogeneity that exists in nature, and so escape its natural enemies for the time being. It can be said that natural enemy activity may well have partly determined the timing of aphid dispersal.

8.1.5 Environmental conditions.

Figure 43 shows that with an increase in age of Sakhalin-fir tree there is a decrease in the number of aphids. Among the reasons given by Yamaguchi (1976) was that aphids are exposed to high temperatures and were not attended by ants. It was found that in summer aphids were restless due to high temperatures, and this was also confirmed by a supporting experiment on the effects of temperature on aphid movement activity. At higher temperatures aphids traveled longer distances than at lower temperatures. Johnson et al. (1957), when studying Aphis fabae, reported that dispersal is a temperature-dependent activity. Aphids fly sooner at higher temperatures. Aphids in plots in open areas experienced high temperatures in summer in addition to the deterioration in the quality of food. Deterioration of host quality may have been caused by aphids, but it is also true that in summer woody hosts are nutritionally less suitable for aphids. Although most aphids dispersed during this period, there are some aphids that remained and were still able to grow and reproduce well on trees. Although temperature influenced aphid movement on the plants, the length of time for which an aphid stays on a leaf depends on its temperature, exposure to sun, frequency with which its underside is brushed by other leaves, its nutritive status and the presence of other aphids (Dixon, 1970; Dixon and Mckay, 1970; Dixon and Mercer, 1983). Although terminal shoot temperatures during summer did not reach lethal levels, most aphids left the upper part and leaves along the stem and lower branches. It is thought that this aphid is not adapted to grow and reproduce on poor-quality nutrition and at high temperatures.

8.1.6 Temperature and light.

In summer aphid movement was very conspicuous in all stages. A supporting experiment on daily dispersal pattern showed that C.todocola mass movement was bimodal, it is somehow related to temperature and confined during early morning and early evening. This finding is in agreement with Johnson et al. (1957). This pattern of dispersal resembles the 2nd generation sycamore aphids present in summer which showed bimodal flight periodicity with a peak in early morning and another after sunset. Haine (1955) and Dixon and Mercer (1983) reported that the low light intensity and temperature thresholds for flight in the species of sycamore aphid enable it to fly early and late in the day, and the decline in aerial numbers at mid-day is associated with high wind speed, which inhibits take off. Flight activity of sycamore aphids increased during sunset, although it is dependent on calm conditions that tend to prevail then, and is heightened by an intrinsic urge to take off at this time of the day (Dixon et al.,1968). The reasons for the bimodal dispersal pattern of C.todocola was not established, although it might be the same as the 2nd generation sycamore aphids. On the other hand the flight activity of the 1st generation sycamore aphids in still conditions is strikingly different, as in this case most take off in the early afternoon when in the field wind speeds are likely to be high (Dixon and Mercer, 1983). This is thought to be associated with their greater tendency to disperse, which possibly serves to transport the aphid further to new habitats.

The green spruce aphid (Elatobium abietnum) has a single flight peak in May just as its host is breaking its buds. The host alternating hop aphid (Phorodon humili) has two peaks like C.todocola and the bird cherry oat aphid (Rhopasiphum padi) has three. The spring and autumn peaks of flight in the two alternating aphids represent the population leaving and returning to the primary host respectively. The same yearly pattern was observed in C.todocola i.e. June/July and September/october dispersal but this may be due to host conditions. Johnson (1969) and Walters and Dixon (1974) reported that aphids are more likely to take off at high than low light intensity and temperatures, and at low rather than high wind speed, but species differ in their responses to these factors. High winds may inhibit take off for a day. It can therefore be said that the patterns of daily movement and dispersal are shaped by the availability of dispersing morphs/aphids and their required light intensity, temperature thresholds for dispersal.

8.1.7 Wind.

All plots were either surrounded by forest trees or nursery hedges, hence the influence of wind was not observed. However, it is assumed that wind has no effect on wingless aphid dispersal since they walk under the trees and are well protected against strong wind. Wind and humidity were regarded as important factors in determining aphid dispersal by flight. Johnson (1969) presented convincing evidence that most aphid migration occurs in windy weather, however, this was for aphids living on annual or short-lived plants, which are often scattered and less apparent than trees. By riding the winds, these species of aphids can scan large areas and so possibly improve their chances of finding other host plants.

8.1.8 Distance.

Distance traveled by different aphid species and different stages of C.todocola aphid differed significantly. C.todocola aphid walking ability was higher than in other species studied and the 3rd instar nymphs of C.todocola walked a longer distance than other stages per given unit of time. Maximum perpendicular distance registered for C.todocola was 16m, although it may be more than this since aphids do not walk in a straight line. However, maximum distance traveled by the 3rd instar C.todocola on a wooden board was 734cm per 30 minutes. It is assumed that this aphid can travel longer distances if it is not inhibited by other factors e.g. presence of grasses, soil texture and structures etc. However the short period for which an aphid can survive without food, its high degree of host specificity, and the random location of host plants may reduce their survival chances. Taylor et al. (1979) when working with hop aphid (Phorodon humuli) showed that migration is not directional, which supports the findings of this experiment. On the other hand, because aphids are opportunists, they adapt at rapidly increasing numbers when conditions are favourable. The simultaneous commitment to growth and reproduction puts a severe constraint, on the length of time of which aphids can spend searching for host plants. Small size and host specificity, both adaptations to feeding on phloem sap, may also impose constraints. Therefore, there is possibly only a short period when dispersal is successful, and the response to changes in day length enable the aphid to synchronize its development to produce sexual morphs which in turn produce overwintering eggs. Survival rates of overwintering eggs are higher than those of aphids that pass winter as instars. Although egg mortality can be very high (Leather, 1981), mortality occurs at a fairly constant rate throughout winter (Leather, 1980; Thornback ,1983). So winter conditions are not important in determination of year to year fluctuations in abundance in holocyclic species as they are in unholoclyclic species. This is one of the reasons why in the second year all eggs laid on plants in the previous year were removed.

The length of time for which an aphid has walked, and the number of trees it has visited, possibly give some indication of the abundance of potential hosts in the forest. The optimal strategy after a long and unsuccessful search would be to settle and feed on the next host plant encountered because of low likelihood of finding a better host especially in a wider spacing and in plots interplanted with non-host trees. In winged species, at the population level the tendency to disperse has been measured in terms of the proportion of the population that develops into alatae (Lamb and Mackay, 1979), and at the individual level, in terms of whether an aphid flies before or after giving birth to offspring (Shaw, 1970a). In C.todocola the second point is applicable but at the population level it is not well known. However, the variability in the tendency of individuals to disperse is also associated with programmed differences in the level of reproductive investment (i.e.. number of ovarioles in the gonads) between individuals. Those with few gonads (like the 3rd instar of C.tococola) take off more readily, and at steeper angles, are more resistant to starvation and have relatively more olfactory organs than aphids with many ovarioles (Walters and Dixon, 1983).

Although Taylor (1965,1974) reported that plants are more colonized primarily by flying aphids, and was supported by Yamaguchi (1976) who also reported that dispersal in uninfested trees takes place mostly by alatae, most of which emerge in the 2nd generation. In this experiment no alatae were produced during the 2nd generation and plants were colonized by walking wingless aphids.

8.2 POPULATION GROWTH

All populations of organisms fluctuate in size. For any population the only affirmation that can be made about it with certainty is that its size will not remain constant. The growth of any population in a restricted environment must eventually be limited by a shortage of resources. Telescoping of generations of C.todocola along with parthenogenesis resulted in an enormous rate of increase.

Aphids can become very abundant, for example in plot 1 October 1993 there were 18105 aphids (equivalent to 405 million/ha), and in July 1994 there were 38904 aphids (126 million/ha). In July 1994, plot 7 and 8 had 126million/ha and 197million/ha., respectively. These values are far below that compared with agricultural aphids. A hectare of beans can produce 4000million alatae of the black bean aphid (Aphis fabae) (Way and Banks, 1967) and the cereal aphid (Meteopolaphium dirhodum) can achieve population densities of1000million/ha of wheat (Dixon, 1975). Although the amount of energy used by C.todocola is not known, it is said that a large amount of energy is used annually by the aphid population. Studies conducted by Llewellyn (1972) showed that lime aphids consume $1.5X10^7JM^{-2}$ yr.$^{-1}$ compared with $3x10^6JM^{-2}$ yr.$^{-1}$ by grazing bullocks (Mcfadyen, 1964) and $6.4X10^5JM^{-2}$ yr.$^{-1}$ for browsing oak tree caterpillars (Varley, 1967). Thus the aphids may extract much more energy per unit area than grazers and browsers, and do so without consuming any of the plant structure. However, of the food ingested by aphids little is used for growth and a lot of the energy is excreted as honey-dew. Food quality was found to encourage population growth of aphids. The greater the nutrient stress experienced by mothers the fewer of their offspring are committed to a high reproductive investment and vice versa (Dixon, 1985).

The following factors were found to influence Cinara todocola population dynamics; food quality, crowding, presence of ants, weather and dispersal. The dynamics of aphid populations, with their overlapping generations between egg-hatch in May and egg-laying in November, the ratio of the densities of this aphid at the two stages may roughly gives a measure of the overall rate of population increase.

8.2.1 Food quality

It was observed that aphids were produced in large numbers from early May to late June, as a result they faced a shortage of suitable food and space. This probably caused intensive intraspecific competition which resulted in the production of fewer and smaller aphids. After the dispersal in July , more space and food were created, and the population was found to increase and the 3rd instar nymphs body weight in late July was a little higher than that in late June. The production of smaller aphids in June could be due to intraspecific competition and deterioration of food quality. In addition to this the quality of sap in trees in summer is not good compared with that in spring. Way and Banks (1967) and Way (1968) reported that many small summer migrants, are produced when aphids are abundant on beans, and intraspecific competition then causes the aphids to disperse. Population studies on the lime and sycamore aphids for 9 and 15 years respectively, showed that even in the absence of natural enemies laboratory populations of lime aphid suffer a sudden decline in numbers, if the numbers are high at the beginning of the season (Dixon 1971a).

The growth and reproduction of aphids is dependent upon the state of growth, or level of soluble nitrogen, in their host plants (Kennedy et al., 1950). Mittler and Kleijan (1970) and Dixon (1970) reported that there is more nitrogen in the phloem sap of plants whose leaves are growing or senescent, because nutrients are then being translocated into or out of the leaves. The sap is not nutritious when the leaves are mature. Thus there are marked seasonal changes in the quality of food available to aphids feeding at a particular time of the year.

The quality of food available from different plants varies. This is an important factor determining the distribution of aphids between plants (Kennedy et al., 1950). It was observed that trees adjacent to infested ones were sometimes not attacked by aphids, and this was thought to be due to tree resistance to attack or nutritional values. There were also trees which were visited two or three times by aphids but were not colonized and this can be explained by low nutrition values.

The ultimate limit to growth over the two years does not appear to be available space, or death of host-plant through over-exploitation, but rather decline in the host quality to a level at which aphid survival is greatly reduced. Barlow and Dixon (1980) when working with lime aphid reported that at lower densities, aphid numbers are regulated by a combination of an increase in the numbers of predators in response to aphid densities early in the year, and at higher densities proportionately more adult aphids disperse which depends on densities experienced during nymphal development. Two population peaks per year could be explained by the fact that the quality of the habitat in which the spring and autumn generation individuals live was good, whereas in the summer generation individuals live in a relatively poor habitat as pointed out before, hence most aphids disperse during this season. On the other hand, Ito (1953) mentioned that in water striders this is done by the movement from ponds of higher density to lower ones.

Although plant resistant to attack varied, in a controlled chamber experiment all trees were observed to drip resin, which is a sign of disease and trees were trying to counteract the effect of aphid by using a defense mechanism. It is thought that, apart from ingesting phloem sap, this aphid probably secreted some disease causing agents. When working with Myzus persicae, Way and Cammel (1970) and Dixon and Wratten (1971) reported that aphids do not merely imbibe phloem sap but they silmutaneously secrete substances into plants that rapidly affect the plant in many cases to the aphid advantages. Both black bean aphid (Aphis fabae) and cabbage aphid (Brevicoryne brassicae) can change the metabolism of their host plants. A few aphids like Myzus ligustrii and Periphyllus aceriola induce a localized yellowing of leaves which become attractive to other species of aphids.

8.2.2 Dispersal.

Dispersed aphids created space and reduced competition for the remaining ones and as a result encouraged their population growth to attain another population peak as it was observed in plots under shade (refer 7.1 above).

8.2.3 Ants.

Ants were found to encourage high aphid population growth by limiting their dispersal through building earth tunnels around their colonies and protecting them from natural enemies. In return ants obtained a rich food supply from aphids (melezitose-trisaccharde). It was also observed that not all aphid colonies were attended by ants and the population growth of these colonies was low and sometimes went extinct. Skinner and Whittaker (1981) reported that ants can have a pronounced effects on the abundance of aphids, for example, number of ant-attended Periphyllus testudinaceus on sycamore are higher on branches foraged by the ant Formica rufa than adjacent branches from which they are excluded. However the other species of aphids on sycamore, Drepanosiphum platanoidis which is not ant attended, does better in the absence of ants (Skinner and Whittaker, 1981). Addicott (1979) reported that of the four aphids on fire weeds three do better, and one worse when on plants that are ant attended. Ant attended Aphis fabae increases its uptake of phloem sap and so increases its production of honey dew by up to 50%. The greater growth and fecundity rates of ant-attended A.fabae are attributed to the improved nutrition resulting from increased feeding (El-Ziady 1960) and to their tendency to disperse less and, consequently, for most of them to aggregate and feed on the youngest parts of their host plants (Banks 1955; Banks and Nixon 1958; Banks and Macaulay 1967). The same was observed in this study, however, at higher population densities plants started to deteriorate and sometimes died out and this could have been due to young plant age/size. It is assumed that in the absence of ants such aphids use more of their resources for dispersal to increase the chance of survival of their clones. At this stage the idea of an inborn trade off between dispersal and reproduction may be considered, with reproduction favoured when the possibility of being killed by natural enemies is reduced.

Newly-founded colonies of Aphis varians and A.helianthi of fire weed, and of Pterocomma populifoliae on aspen, are more likely to persist if they are found and attended by ants within the first week. Exclusion of ants causes such colonies to go extinct faster than ant attended colonies. This is due to the ants attacking and killing aphid predators (Sanders and Knight, 1968; Addicott, 1979). Similarly the ant Lasius niger affords small colonies of A.fabae protection against a range of natural enemies (Banks, 1962).

As ant attendence can result in rapid increase in the size of the aphid colonies, as well as a 50% in increase in the rate of feeding of the individual aphid, the combined effect could be a more rapid deterioration in the quality of the host plant for the aphid as was observed in this experiment. It is likely that it is this, rather than the presence of ants, that results in the decline of the larger colonies. Way (1963) reported that in those species of aphids that are only found in association with ants it is possible that the ants keep the aphids at densities below that which is harmful to their host plants, and may even keep the total number at levels that satisfy the food requirements of the ant colony. In this study ants were observed to carry aphids from the terminal part to the butt area during summer. It is not clear if ants were protecting aphids from high temperatures, hiding them from natural enemies or preying on them (regulating their numbers). However, Sakata (1994) reported that ants preyed less on aphid species which they attended, but increase in aphid density per ant led into aphid predation.

Addicott (1978) reported that in foraging for honey dew, ants are likely to be attracted to the richer sources, only exploiting poor sources when honey dew is in short supply. Thus there could be competition between aphids for ants. Therefore, colonies are likely to go extinct if they are close to plants occupied by ant-attended aphids as mentioned above. In addition there is some evidence that ants switch their attention to other species of aphids as a source of honey-dew when the number of favoured species of aphids decline. The ability to produce melezitose (trisaccharide) and other trisaccharides which are particularly attractive to ants (Duckett, 1974) has been selected for because ant attendance has advantages for aphids (Kiss, 1981). Production of Meleziotose does not guarantee aphid attendance, the lime aphid Eucallipterus tiliae produces this trisaccharide but it is not ant-attended. Aphids convert mono- and disaccharides into trisaccharides like melezitose, which reduces the number of molecules in solution and thus its osmotic concentration, however, the concentration of melezitose present in honey-dew is 45% (Michel, 1945, Bacon and Dickson, 1957). Therefore, ants can have pronounced effects on the abundance of aphids, as was observed in plot 1 and 7 in 1993 and 1994 respectively. Thus the dynamics of the colonies of ant-attended species of aphid are very much dependent on the availability of ants. Un-attended colonies, are more likely to decline than attended colonies.

In controlled chamber experimental populations, the density-dependent factors operated first, and emigration and the reduction in the fecundity of the aphids as a result of crowding and poor food quality experienced during their development operated next.

8.2.4 Weather.

Aphid population densities were observed to be regulated by environmental factors such as temperature, rainfall and to a lesser extent wind. Weather affects the system through its effects on aphid rate of increase, successful colonization of plants and the activity of its predators (Way, 1967) Weather can also be taken as a disturbing factor and as a major determinant of peak numbers, and number of fundatrices through egg mortality. Weather through its effect on the aphids rate of increase and colonization of plants can modify this pattern as can the activity of natural enemies (Way, 1967). It was found that the greater the number of aphids produced in May/June the greater the number of dispersing aphids in summer. It was also interesting to note that the high level of abundance in June/July is followed by low numbers in September/October and vice versa. This trend was also observed in one species of host alternating aphid and three of autoecious tree dwelling aphids (Dixon, 1985).

The effect of wind was not observed in this study since all the plots were surrounded by hedge or trees and aphids walked under the planted saplings which gave them additional protection. It is thought that air currents may have caused limited death to aphids by brushing leaves. However wind is said to be a disturbing factor through its effect on mortality, both in lime (Eucallipterus tiliae) and sycamore aphids (Drepanosiphum platanoidis). Temperature also caused fluctuations through its effects in flight in the lime aphid (Dixon, 1979; Barlow and Dixon, 1980). Wind caused leaves to brush together, which dislodges the aphids, most of which are then lost to the population (Dixon and

Mckay, 1970). Therefore wind can act as a device converting weather into aphid mortality.

8.2.5 Temperature.

Among environmental variables that influence insect population growth, temperature is one of the major factors (Barlow, 1962). In summer aphids were found to be restless and it was thought that aphid dispersal was a result of hot temperatures. Temperature causes fluctuations through its effects on dispersal in the lime aphid (Dixon, 1979).

8.2.6 Natural enemies.

The number of predators and parasites reported in this experiment was very low (3 species) compared to 24 species of 8 families reported by Yamaguchi (1976) and 6 families reported by Furuta (1976). This could be due to the fact that this plant species is indigenous to Hokkaido where natural enemies have established. The effects of predators on populations was not observed. Although predators and parasites can inflict heavy mortality on the aphid (Banks, 1955 and Way and Banks, 1968), the numbers of the aphids are not regulated in this way. Furuta (1976) reported that at high aphid population densities the effects of predation on C.todocola aphids was negligible, and this could be due to parthenogenetic reproduction and high fecundity and overlapping generations of this aphid. In this study hunting (predacious) spiders were the only effective predators checking establishment of the aphids which emigrated on host trees or those escaping from ants nests, which is in agreement with Furuta (1976) and Yamaguchi (1976).

8.2.7 Sexual production.

Sexual morphs were produced during the last generation. Aphids are thought to synchronize their life cycle with the growth and development of the host plants. This may be true since Yamaguchi (1976) reported 7 or 8 generations per year and Furuta (1976) 8 generations per year. Parthenogenetic reproduction continues as late as is compatible with successful egg laying. However, 40 years ago Bonnet proved beyond reasonable doubt that aphids may propagate without fertilization and continue to do so for as long as 10 generations. Therefore Furuta's value is within an acceptable range. Huxley (1958) was the first to show that if aphids were kept warm and supplied with food they could reproduce parthenogenetically without deterioration, apparently indefinitely. This is also supported by the existence of many unholocyclic species aphid. Huxley's theory is only applicable in a controlled conditions. However, the role of photoperiod in the induction of sexual forms in producing genetic diversity individuals is widely known. At the onset of autumn in temperate regions many species of aphids switch to the production of sexual forms, with each clone producing both egg laying females (oviparae) and males. Although associated with short days the switch is usually triggered by long nights (Lees, 1973). Lees(1979) confirmed that when aphids are exposed to short day regime, the appearance of males (winged) and oviparae is delayed from 75 to 90 days irrespective of generation number. His finding is in disagreement with the laboratory experiment, whereby winged aphids were not produced irrespective of the long day length. Forrest (1970) reported that in several aphid species sexual production occurs in response to changes in the host plants. In temperate regions the short day conditions in autumn induces plants to cease growth and become dormant. This argument indirectly supports the day length effect in the production of sexual morphs. It is important to know why this aphid produces sexual morphs. Sexual reproduction generates offspring with a range of genotypes which include those fitter for a particular patch than offspring produced from a single genotype. This also improves the chances of survival of a species in a heterogeneous and changing environment. The genetically similar individuals of an asexual offspring have the same ecological requirements and will compete severely with one another. Asexual reproducing parents reduce this competition by producing genetically different offspring (Young, 1981). Therefore in autumn, further increase in population numbers is restricted by shortage of food and low temperatures (and aphids enter a resting stage) at this time the production of overwintering eggs provide an excellent opportunity to reproduce sexually, since an egg needs not to be in an advanced stage of maturation to survive. Ward et al. (1984) reported that in holocyclic species the sexual generation is the last in the season which produces the resistant eggs.

8.2.8 Food

Aphid population growth after hatching in May was very high and then the rate of growth declined with time and after dispersal population growth picked up around August/September. This is thought to have been caused by the fact that, in May when eggs hatch, food was abundant and of high quality, and natural enemies were scarce. Under these conditions parthenogenesis was favoured.

8.2.9 Aphid size.

The weight of the third instar nymphs produced in early generations was higher than those that were produced in later generations, and this was thought to be a direct consequence of the poor quality of food available to aphids in later generations, competition, high temperature and the decision made by the reproducing mother whether to produce a dispersing morph or a reproducing morph. It was found that the 3rd instar in July after dispersing was heavier than those produced in June.

Although small size is a feature of aphids ever since their evolution, even so there is range of size within a species. In general larger sized (like stem mothers) organisms have a better chance of reaching a reproductive condition and then tend to produce more gametes (Carlow, 1978). Therefore, it is important to consider what determines size in aphids.

It has been reported that small individuals develop when they are reared in crowded conditions, on mature plants, or at high temperatures, and a large ones result when nymph are reared in isolation, on young, or senescent plant or at low temperatures. Therefore, the effect of food quality on size is not suprising. Muller (1966) postulated that size in aphid is a balance between catabolism and anabolism. At higher temperatures catabolism consumes most of the available energy, and little is left for growth. Similarly, an imbalance in the energy requirements of basic metabolism and growth has been proposed to account for the smallness of certain Lepidoptera when reared at a high temperature (Marthavan and Pandian, 1975). Small size in Myzus persicae at high temperatures has been attributed to an adverse effect on the aphid symbionts (Lawson, 1941) and resultant deterioration in the quality of food available to the aphid. By treating development and growth separately, Chambers (1979) showed that although aphids reared at high temperatures are small, they nevertheless have a higher growth rate than those reared at low temperatures, this is also supported by Yamaguchi (1976). It can be said that size is a consequence of the relative effect of food quality and temperature on growth and development. An inverse relationship between size and temperature is wide spread in insects. According to Dixon et al. (1982) aphids small at birth are slow to reach maturity and this may reflect the early stage of development at which these aphids are born.

Food quality and temperature have a marked effect on aphid size. Poor food quality and high temperatures result in small aphids, as a consequence of the effect of these two factors on aphid development and growth rates. Thus in sycamore aphids aestivation is in summer in response to the harsh conditions of summer (Dixon, 1985) and the same was observed in the maple aphid (Hashimoto and Furuta, 1988). It can therefore be said that for each species of aphid there is possibly a limited range of food quality and temperature over which it can increase in numbers. At high temperatures aphid relative growth rate declines as does its respiratory rate and honey-dew production, and associated with this is an increase in mortality. When feeding on a good quality host, sycamore aphids increase in weight and vice versa and can only fly from a good quality host after reducing their weight. This is achieved by excreting several drops of honey-dew (Mercer, 1979). From the above argument it can be said that low aphid body weight in later generations was due to food quality, competition and high temperature.

8.2.10 Alatae

Most authors associate the production of winged aphids with crowding, food quality, and change in the day length with an ultimate purpose of dispersing. Yamaguchi (1976) pointed out that the production of winged C.todocola in the 2nd generation is density-independent with the sole reason of dispersing. Although in this experiment and in Furuta and Aloo (1994) winged female aphids were not observed, however, in October (autumn) winged males were produced. The production of males was thought to be due to food conditions, short day length, crowding and intrinsic factors. Alate production and dispersal has been regarded as means of regulating numbers, and in several species it is most marked when there are large populations, however, the production of alates at a particular time of the year, even when aphids are reared in isolation, reveals that the primary role is dispersal (Dixon,1985; Matsumoto, 1988; Ozaki,1988; Furuta and Takai, 1983), and this is supported by Yamaguchi's (1976) finding. By responding to a number of stimuli rather than one, aphids can possibly achieve a closer and more reliable tracking of environmental conditions. This enables them to produce the more fecund and faster developing apterae while a host plant is fovourable, and when it becomes unfavourable to switch gradually to producing dispersal morphs that can disperse to other plants.

Although not found in all aphids, in vetch aphids (Megoura viciae) it is the tactile (touch) stimulation associated with crowding that induces the development of winged forms. Lees (1967) proved that crowding resulted into the production of alatae. When several apterous mothers that has been reared in isolation are confined together in a small glass tube for 24hrs and are then placed individually on bean plants, they give birth to alates. However, apterous mothers confined individually in glass vials for the same period give birth to only apterous offspring. This type of behaviour was also reported by Shaw (1970) when working with Aphis fabae, Dixon and Glen (1971) and Watt and Dixon (1981) on Rhopalosiphum padi and Sitobion avenae respectively. The more intense the crowding, the higher the proportion of alates that develops especially if both mothers and offspring experience crowding. In this experiment the number of winged males increased with an increase in population size, therefore crowding may be one of the factors. By responding to cues that indicate an impeding deterioration in habitat quality aphids can switch to reproducing alatae in advance of the adversity taking place (Lees, 1979). The decision is made just before birth. The appearance of winged males in October is supported by Bonnemaison (1951) who reported that sexuals rarely appear in the field before autumn. This is because of the operation of an intrinsic timing mechanism, and Lees (1960, 1966) termed it as an internal time.

The effect of plant organs on alatae production was shown by Watts and Dixon (1981). When mothers of English grain aphid (Sitobion avenae) reared on the ears of grasses at flowering are crowded in glass vials for short periods they give birth to proportionally fewer winged offspring than mothers similarly treated but reared on matured ears. Similar observation were made on pear aphid (Acythosiphon pisum), but rosy apple aphid (Dysaphis devecta) can even produce alatae solely in response to change in host quality (Sutheland, 1969; Forrest, 1970). When rearing nymphs and adults of Myzus persicae in isolation on a synthetic diet, Mittler and Southerland (1971) found that the composition of food partially controlled wing polymorphism in this species.

Forrest (1970) complicated the issue of the influence of food quality on the production of alatae. He reported that, although apterae tend to develop mainly on good food, a high proportion of apterae develops on poor diets if before giving birth, their mothers are allowed to walk on and superficially probe the surface of a nutritionally good host plants. In this case it can be said that some features of the plant surface acted as a token stimulus of a good quality. Therefore, the decision on which morph to be produced is based on mothers just before giving birth. If this argument is true winged aphids in the 2nd generation of the winged C.todocola aphids (Yamaguchi, 1976) could have been due to poor food quality at that time just before reproduction. The above argument is supported by Mittler and Kleinjan (1970) who reported that very poor synthetic diets allowed mainly apterae develop in Myzus persicae. Also other aphids developing on poor-quality hosts were similar (Schaefers and Judge, 1971; Dixon, 1972). Lees (1966) brought a theory of a biological clock mechanism in aphids that inhibits the production of alatae, not only by the founding mothers but also her apterous daughters. This refractory phase is time dependent and not generation dependent. Therefore the production of winged males is thought to be caused by day length since no winged males were produced in a controlled chamber although food condition was very bad.

At this point it is difficult to accept the issue of food quality suggested by some authors above. Most literatures have pointed out that alatae are produced at a definite time of a year. This is particularly so far for the alate gynoparae and sexuparae that give rise to males and females in autumn. The proportion of green spruce aphid (Elatobium abietinum) that becomes alatae is influenced by crowding, host quality and temperature, the dominant factor is the increase in the day length in spring (Fisher, 1982). Increased alatae production in response to changes in day length has been reported for Myzus persicae (Matasuka and Mittler, 1978) and in C.todocola (Yamaguchi, 1976).

It is still very important to know why alate females were not produced. Although it was reported above whether to produce alates or not is a decision made just before giving birth and is based on the food quality. The other reason could be on the cost and benefit basis. Aphid must decide whether it is profitable to produce a dispersing or a reproducing morph. Dispersal morphs especially alatae, generally take a longer time to reach maturity, are small and less fecund than apterae, especially in poor habitats, and if very small, they are poor fliers. Therefore, in very harsh conditions it would be advantageous for a clone to produce apterae better able to survive until conditions improve, rather than allocate limited resources to dispersal. Actually this is thought to have been done by the aphids in an open area plots, unfortunately these aphids may have miscalculated and gone extinct.

8.2.11 Feeding area.

Cinara todocola was first observed to feed on the terminal parts of the plant then shifted into other parts, especially lower parts in open area plots. This could be caused by differences in the quality of phloem-sap, and temperature. In plots under shade, shifting of position may have been caused by competition, and climatic conditions especially temperatures and rainfall. It was reported that the spatial separation of aphid species on the same tree does not prevent them from competing. Although feeding positions on a plant may be not overlap, nevertheless aphids are feeding on a common resource-phloem-sap. Intraspecific competition for this resource may be intense and result in longer developmental times, smaller aphids or a switch to the development of another morph, more better adapted to dispersal (Addicott, 1988). The interspecific effect on alate production is less than the intraspecific effect. In 1994 some saplings were infested with spittle bugs and C.todocola left those plants. It is thought that spittle bugs prevented the colonization of the tree by C.todocola. Stroyan (1977) reported that the rain honey-dew from Chromaphis junglandicola that feeds on the underside of walnut leaves was thought to prevent the colonization of the upper surface of the leaves by Calaphis junglandis. This could be called interference.

8.2.12 Aphid and plant.

The mutualism between ants and some aphids species is well established, but between plants and aphids is not yet known. It is widely known that the aphid is a parasite to plants, and when carrying disease causing agents may transmit diseases to plants which can affect plant fitness. Although aphids are adapted to its host, there is little or no evidence on what benefit plants get from aphids. Production of excess honey-dew leads some authors to think about the benefits plants get. Owen (1978, 1980); Owen and Wiegert (1976, 1981) proposed that plants benefit from being eaten and in particular, plants benefit surplus sugars by enlisting the help of aphids. The sugar in the form of honey-dew is utilized by free living fixing bacteria in the soil, which increase in number beneath aphid-infested plants and make more nitrogen available to these plants. Dighton (1978a,b) reported an increase in the abundance of microbial populations, at least in woodland soils and sugars found in honey- dew are more effecient at promoting nitrogen fixation (Pettetle, 1980). It is thought that aphids are a necessary part of plant releasing surplus sugars that promotes a better supply of nitrogen. Infested oak and sycamore trees leaves become dark green. In oak this is a consequence of a 25% increase in the quantity of both chlorophlly A and B. Associated with this is an increase in dry matter production, which is in sycamore can be 1.7 times greater than uninfested leaves (Dixon, 1971b & 1971d). Aphids provide higher levels of nitrogen fertilizers to cereals, however, they do affect plant reproductive potential. In a nutrient rich environment aphid infested plants grow more slowly than uninfested plants (White, 1970). There is no evidence to support the contention that plants infested with aphids are fitter than those that are free of aphids. However, Ozaki (1988) found that height and height increment of the infested trees were significantly higher than those of the uninfested ones.

8.2.13 Ant attended aphids.

The influence of ants on aphid population growth has been dealt with above. Some reasons were also given as to why some trees with aphids were not attended. Aoki's (1975 and 1977) exciting discovery of morph soldier in Colophina spp. and Pseudoregma alexanderi (Pemphiginae) may give insights as to why some aphids were not attended by ants. Sataka et al. (1991) also reported the existence of sterile soldiers in the bamboo aphids (Pseudoregma bambucicola). Although it is not true to say that the aphid is a social insect, but the discovery of a division of labour is one step ahead. It was reported that 13% of a colony are soldiers, which are short lived do not eat or reproduce and defend the colony against insect enemies. Although the functions of the morphs especially the first instar was not studied, it is thought that those trees without ants might have morphs that defended the clone. It was reported that larger aphid colonies with soldiers are not attended by ants. Since the decision to produce alate or apterae is done by laying mothers just before giving birth based on perceived conditions, it is also thought that if a colony is not attended (protected) by ants the production of soldiers may be triggered by the laying mother sensing the need to produce defenders as well as producing winged (dispersal) morphs.

It was also observed that individuals of each morph are involved to a varying degree in defense, dispersal, reproduction and survival (Aoki, 1980). However, specialization in one or other of these functions may impose constraints in terms of resource allocation, physiology and structure for carrying out the functions. At a certain time particular functions are more important than others for survival, and this has resulted in the evolution of the division of labour within a clone that is reflected in its polymorphism. Individual large aphids are capable of defending themselves against a wide range of natural enemies. An aphid may kick, walk away, drop off the plant or smear wax over an attacker which is often accompanied by release of an alarm pheromone that alerts nearby aphids. Aphids respond to these volatile substances by vacating the area (Dixon, 1958). This is thought to have happened on trees with syrphid larvae.

Aoki and Makino (1982) observed the 1st instar fundatrices of a gall forming aphids with a heavy sclerotization that affords them protection against attack by other individuals. Approximately 50% of 100-200,000 aphid inhabitants of the large galls produced by Aegopteryx styracicola on snow ball trees are biters (Gailer, 1956; Aoki et al., 1977; Aoki, 1979). The proportion of biters or soldiers in a colony, and whether they are sterile, possibly depend on the probability of attack by natural enemies, and the decision to produce a soldier is done by the mother possibly just before depositing a young one as was explained above on the production of alatae for dispersal.

Division of labour, increasing the chances of survival of a clone, may also occur within a morph. For example in the gall forming aphid Pemphigus dorocola, the first instar fundatrigenia have a cleaning role (Aoki, 1980). However, it is not documented whether this instar has special morphological adaptations to carry out this cleaning function.

8.3 Dispersal by walking.

Although it has been proved experimentally that C.todocola walked longer distance per given time than other aphid species it was compared with, and the 3rd instar nymphs also walked longer distance than the other stages, it was not proved if they have any morphological or physiological characteristics that support this argument. It is important to know the proportion of body that on average makes up the locomotory apparatus especially for the 3rd instar nymphs. In Rhopalosiphum padi, Drepanosiphum platanoidis, Callaphis jungladis, Megoura viciae and Tuberolachnus salignus during dispersal it is approximately 40% (Dixon ,1985).

9.0 CONCLUSION

The tendency to disperse is an evolved adaptation (Johnson et al., 1969) that has enabled aphids to spread the chance of survival in space and seek out and colonize plants that are above average quality. Wider spacing between plants prevented/delayed the spread of aphids (Furuta and Aloo, 1994), although they did not propose optimal planting spacing for optimal land utilization. In order to economically maximize land use and at the same time reduce chances of infestation, interplanting with a non-host plant may be a better alternative. Planting two species in the same area may cause some management problems such as running two management plans on the same area. Each species will need different silvicultural treatments at different times of the year, and this may be too costly. Most of the Japanese forest plantations are monoculture, and this is very dangerous, especially when the forest is attacked by a disease or insect such as the attack by pine wood nematode on red pine (Pinus densiflora). It is better to incur a cost today than loss after 40 or 50 years later, and this may be done by diversifying the forest. When an aphid is dispersing in wider- spaced plots chances of locating a host plant is reduced, and if interplanted with non-host trees chance of locating a host is further reduced, and on the other hand increases the chances of being preyed on, getting lost or dying due to hunger. Dixon (1985) reported that the short period for which aphid can survive without food, their high degree of host specificity, and random location of host plants is a constraint in colonizing many plants. It was reported above, before dispersing aphids have to make decisions on the risks of inbreeding and outbreeding. The costs of outbreeding are being lost and dying, or being preyed on by natural enemies. Therefore, to maximize land use at the same time reducing infestation 3m spacing interplanting with non-host plants is suggested. In natural forests, although natural enemies are well established, beating up (replanting) should be done using different plant species with an ultimate aim of creating a species diversity forest.

Winged male aphids were not produced in the controlled chamber experiment although food condition was very bad. This led me to think that the production of sexual morphs was not related to food condition as was proposed by many authors. This finding may support Huxley (1958) who reported that if apterous mothers are given good quality food they will continue to reproduce parthenogenetcally indefinitely and Ward et al.(1984) who reported that parthenogenetic reproduction will continue until time for sexual reproduction is suitable. This experiment supported the influence of day length on the production of sexual morphs in autumn as reported by most authors. A threshold for mass dispersal in this experiment was found to be from 300-400 aphids on a 55cm (mean ht.) tall Sakhalin-fir sapling. Although deterioration of host could be a cause for mass dispersal the primary cause might be high density. Exudation of resin could have been caused by secretion of foreign bodies into plants by aphids as suggested before by Dixon (1985), and by trees growing under stress. Aphids shifting positions as observed could be due to differences in phloem sap quality as mentioned earlier. Dispersal was found to be caused by crowding, deterioration in host plant condition or both.

The striking walking ability of the 3rd instar nymphs lead me to speculate that the function of this aphid in a clone is dispersal. Usually resources are scarce and there are advantages in putting more dispersal resources to one stage than all stages. The tendency to disperse depends on reproductive investment (number of ovarioles in gonads) between individuals (Johnson,1969; Shaw, 1970c) within a clone, and this is independent of their size. Those with few (as the 3rd instar) ovarioles tend to disperse more. It is thought that the 4th instar nymphs had already invested in reproduction and so had low tendency to disperse. Higher walking ability of the stem mothers could be due to its body size. Dispersal powers differ widely according to the inherent capacity for active locomotions and susceptibility to weather conditions. Adaptation in the species occurs both as a result of selection and of induced factors, such as food preferences transmitted from parent to progeny.

Aphid movement was proved to be random. Dixon (1985) proved mathematically that aphids are mostly monophagus and find their host plants by random search. Hirano et al. (1993) reported random movement of adult females of Thrips palmi. Taylor et al. (1979) reported that aphid dispersal is not directional.

If it is agreed that locating a host is a random activity as reported by Dixon (1985), then the question of aphids being attracted to colour may contradict this random theory. This could be true due to the fact that most authors have reported that after settling on a plant an aphid recognizes a potential host by the structure and chemistry of its surface and internal tissue. It ingests some sap and when ingesting sap of a non-host plant which is non-nutritious it leaves the plant immediately. Therefore, this suggested that locating a potential host is by taste and not by visual cues. Hirano et al. (1993) reported that thrips do not use air borne chemical cues of plant in long-distance searches for food plants and it is still not known if there are some phytochemical cues contributing to short range host searches. This means that it located its host by chance, since it leaves the plant after sap ingestion. There is also an argument that yellowing of plants attracted aphids, although this might be true, it may also be true that it is a coincidence that in the cause of probing it happens to find a yellowish senescent plant. In autumn most aphid species disperse and this coincides with the yellowing of plant leaves. Until now there is no paper that has objected to aphids being attracted to yellow colour. Colour is a good indicator of nutritive status of a plant as both highly nutritious young and senescent foliage tend to be yellower than the nutritionally poorer mature leaves.

In this experiment it was found that green colour attracted more aphids than yellow. Kennedy (1976) reported that aphids fly upward in response to the light from the open sky and fly downwards in response to light reflected from vegetation. Although the colour of vegetation was not mentioned it is obvious that vegetation colour is green. It was also reported that aphids can control their landing on plants and respond to their olfactory or visual cues or both, probably landing on a green plants. Kennedy et al. (1961) supported the argument that aphids respond predominantly to visual cues, showing a marked orientation to yellow.

Ploughing the forest or leaving the forest floor with vegetation may prevent/delay aphid dispersal. Taylor et al. (1979) showed that aphid dispersal is not directional. Therefore, this silvicultural treatment may further reduce chances of aphid infestation.

Cinara todocola moved longer distances by walking than other aphid species it was compared with at both lower and higher temperatures. It was proved that with the same body weight C.todocola moved longer distances than other aphid species. Therefore, it can be said that this aphid is adapted to walking compared to agricultural and herbaceous aphid species. Although agricultural and herbaceous aphids are found near the ground surface, due to the nature of their host plant (annual/short lived) and their biology, they do not disperse by walking apart from walking on their host plants. Dixon (1985) reported that minor movement and within and between adjacent plants is mostly undertaken by apterous. In agricultural and herbaceous plant leaves of adjacent plants do touch each other as in the 0.3m spacing plot (Furuta and Aloo, 1994) hence inter-tree movement is just like within plant movement.

It is not clear as to why aphids showed daily bimodal dispersal. A bimodal pattern of dispersal in early morning and sunset in the 2nd generation sycamore aphids and other tree dwelling aphids was due to the fact that winged aphid flight is inhibited by low light intensity in the night and low temperatures during the day (Johnson et al. 1957). Haine (1955) and Dixon and Mercer (1983) elaborated by reporting that the low light intensity and temperature thresholds for flight in sycamore aphid enable it to fly early and late in the day and low numbers at midday are associated with high wind speeds which inhibit takeoff. And the dramatic increase in flight activity around sunset, although dependent on the calm conditions that tend to prevail then, is heightened by an urge to take off at this time of the day. Aphids are likely to leave at high rather than low light intensity and temperatures, and at low rather than at high wind speeds. However, species differ in their responses to these factors (Johnson, 1969; Walters and Dixon, 1974). Since wind has no effect on the dispersal of this wingless aphid it is assumed that temperature and light intensity contributed to their dispersal.

9.1 Future research priorities

In his studies, Yamaguchi (1976) reported production of winged females during the 2nd generation, however aphid population in this study and the one studied by Furuta and Aloo (1994) did not show any winged female morphs. This fact suggests that there must be some genetic differences in those two populations. Therefore the studies using genetic markers may clarify the differences between Hokkaido and Tanashi populations.

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Appendix 1. Life cycle and morphs (After Yamaguchi,1976).

1. 世代，繁殖経過

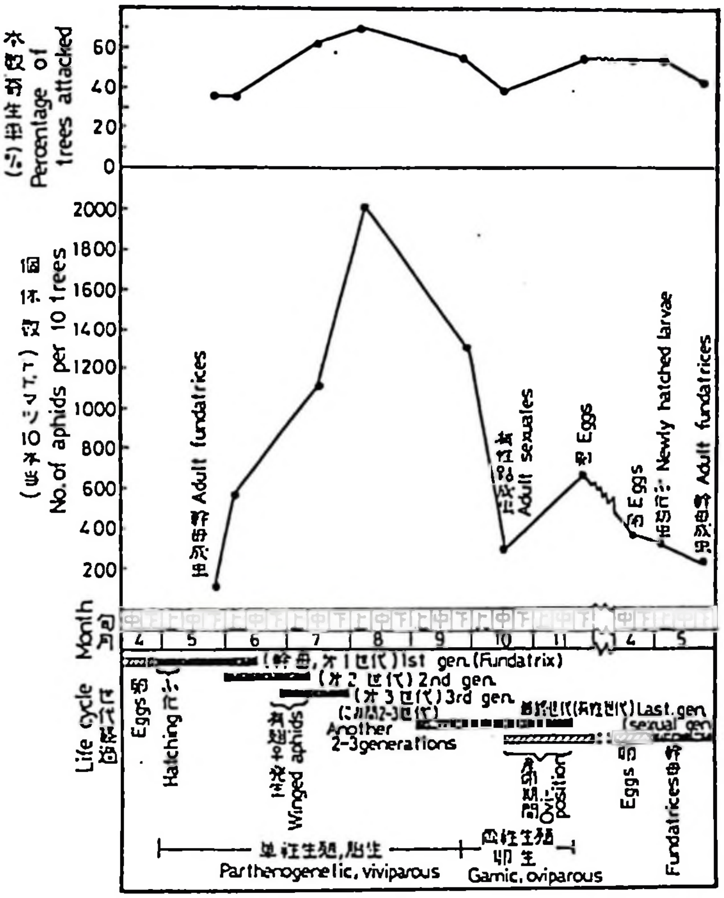

Fig. 1 トドマツオオアブラの世代経過と個体数，本数寄生率の季節的変動（野幌，1963〜1964年）
The life cycle of *Cinara todocola* and seasonal changes of the population density and percentage of trees attacked in a young plantation.

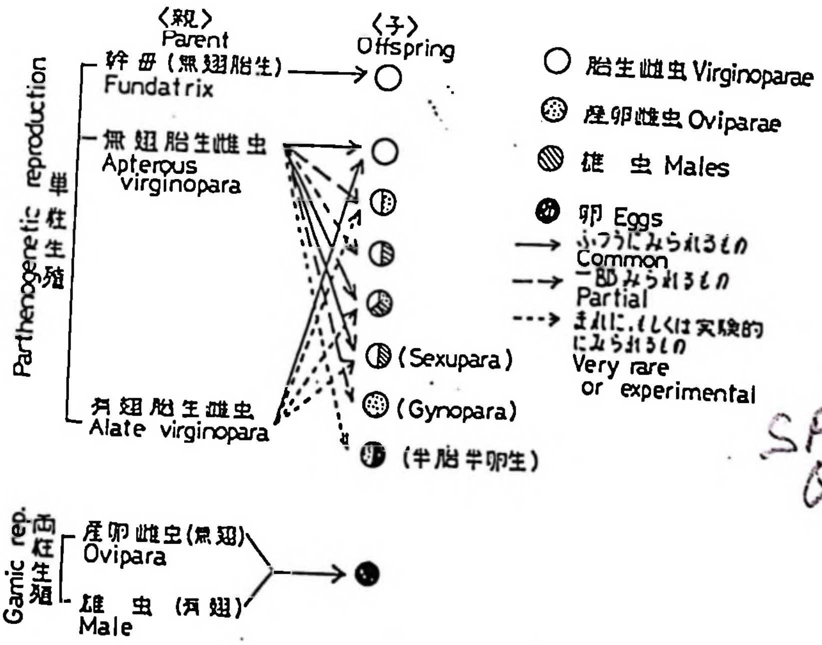

Fig. 2 トドマツオオアブラにおける多型と繁殖にみられる親子関係
Morphs and reproductive capacities observed in *C. todocola*.