MOVEMENT AND DISTRIBUTION ~~BEHAVIOUR~~ OF THE CASSAVA GREEN MITE, *MONONYCHELLUS TANAJOA* ~~(BONDAR)~~ (ACARI: TETRANYCHIDAE) AND ITS ~~PHYTOSEIID~~ PREDATOR, *NEOSEIULUS IDAEUS* ~~(DENMARK & MUMA)~~ (ACARI: PHYTOSEIIDAE) ~~WITHIN THE CASSAVA PLANT~~

ON CASSAVA

THE MITE,

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ABSTRACT

The behaviour of the Cassava green spider mite (Mononychellus tanajoa) and that of its predatory mite Neoseiulus idaeus was studied in both laboratory and glasshouse conditions.

All CGM age-groups tended to emigrate from the leaf of introduction. However the extent of emigration depended upon the age-group, density, leaf age and condition, and the presence or absence of CGM slurry.

The main emigration occurred within the first 6 hours. All adults, except females on young leaves, dispersed at a significantly greater rate than the immature groups on all leaf treatments.

When all age-groups were present on the same leaf, males still had the most emigrants. Within the leaf, all age-groups were significantly more abundant on the palm than the middle or distal portions. This distribution was true even when all age-groups were together on the same leaf.

The mites spent the greater proportion of the 15 minutes on the lamina, and the speed of each group did not differ when individuals were alone on the experimental leaves. However the speed of all the groups (except males) was significantly reduced when crowded compared with solitary individuals.

The distribution of adult females tended to be skewed toward the upper half of the plants. Most redistribution took place when the mites were released at the bottom and middle leaves whilst little movement occurred down the plant when released from the top.

With the predatory mite N. idaeus the emigration behaviour of adult

females was similar to that of the deutonymphs at densities 15 and 25, but differed at the lower densities (i.e. 5 and 10) when more females emigrated than deutonymphs.

The activity of N. idaeus studied when starved for 0, 12, 24 and 36 h did not differ between starvation categories although the phytoseiids at the higher categories tended to visit more leaves than at the lower starvation regimes.

The distribution of the phytoseiids on plants where CGM were present tended to be similar between the lower and the upper parts of the plants whether the phytoseiids were released on the top or on the bottom-most leaves. More phytoseiids remained on the lower half of the plant than on the upper part when the releases were made on the middle leaf.

The majority of phytoseiids dispersed away from the plants regardless of the site of release; however fewest remained when the release was on the bottom-most leaves.

The results are discussed in the light of previous published work.

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SECTION 1. GENERAL INTRODUCTION

SECTION 1

GENERAL INTRODUCTION

Cassava is grown throughout the tropical regions of the world and is important in the cropping systems of Africa south of Sahara, providing carbohydrate for more than two hundred million people. The popularity of cassava lies in its ability to withstand drought when other crops, such as maize, die and also that it performs well under the management of small farmers (Cock, 1982; Hahn & Keyser, 1985).

The dietary importance of cassava in Africa and its increasing importance as animal feed world wide (Leuschner, 1980) and its industrial uses (Hammond, 1977; Robinson & Katianawa, 1979) are all threatened by the introduction of such pests as the cassava green spider mite, Mononychellus tanajoa (Bondar) and the mealybug, Phenanococcus manihoti Matile-Ferrero.

The cassava green spider mite (CGM) was accidentally introduced into Africa from South America nearly two decades ago (Lyon, 1973) and is now one of the major pests of cassava in Africa (Yaninek & Herren, 1988). It belongs to the family Tetranychidae to which a complex of other cassava feeding spider mites also belong (Bellotti & Schoonhoven, 1978a). CGM is of considerable economic importance (Bellotti & Schoonhoven, 1978b), even being considered by Nyiira (1982) as the most destructive tetranychid pest of cassava, although Rodriquez (1978) considered it second to Tetranychus urticae (Koch) as a pest of cassava from a world wide point of view.

CGM feeds on the under surface of cassava leaves by inserting its stylet into and sucking the contents of individual cells. Such feeding

activity can cause 60+% damage to the leaf chlorophyll and about 15% reduction in the leaf area (Ayanru & Sharma, 1983) and therefore reduces the photosynthetic area of the leaf (Cock, 1978).

Precise losses of yield resulting from the feeding activity have not been determined under field conditions, although estimates have been given by a number of researchers, and losses as high as 46% have been reported from Uganda (Nyiira, 1976). Bellotti and Schoonhoven (1978b) have also indicated that CGM will reduce yield of cassava leaves, which are consumed as a potherb in many parts of Africa (Hahn, 1982).

The distribution of CGM on the cassava plant is highly skewed towards the upper part, where the leaves are younger (Yaninek, 1985), with the highest numbers being recorded from the top 5-10 leaves, with fewer on the top 3-4 newly flushed leaves (Yaseen & Bennett, 1977). Similar distributions were observed by Nyiira (1978) on 3-15 month old cassava. This distribution appears to be associated with both nutritional and physical aspects of the foliage. Plant nutrition, for instance fertilizer and soluble salts in the soil, was correlated with increased numbers of T. urticae (Kuenen, 1949; Bandarenko, 1949; Rodriquez & Neiswander, 1949). Nyiira (1975) observed that high population densities and the physical condition of the leaves influenced the distribution of CGM within a plant. Changes associated with ageing, unfavourable surface hardening, drying, wax deposition and inherent changes in the nutritive composition may also be involved in determining their distribution (Van de Vrie et al., 1972). Dispersal of CGM (as with other tetranychid mites) results in the expansion of the range of the species through colonisation of new habitats, reducing the risk of extinction from local catastrophic events. The rapid spread of CGM in Africa indicates their efficiency in both short and long range dispersal. Movements through infested material, wind and air currents have been

suggested as the main causes of spread (Yaninek & Herren, 1988). Aerial dispersal by tetranychids has been established by a number of researchers (Fleschner et al., 1956; Boyle, 1957; Osabake, 1967). Yaseen & Bennett (1977) found that the wind dispersed CGM about 200 kilometres in 13 days.

When the dietary importance of cassava to man and its industrial potential are considered, control of CGM becomes vital. However, following the discovery of CGM, control was not initiated immediately because the mite was unknown to the majority of farmers (Yaninek & Herren, 1988). Attempts were made, however, to screen chemicals for use against the pest, but the subsistence level of the crop and the social and economic constraints associated with the use of such chemicals, combined with their undesirable consequences, limited the choice for adoption (Nyiira, 1972, 1976; Yaseen, 1977). In addition, cultural measures available to farmers were few, and labour constraints for many farmers limited the implementation of some suggested practices such as early planting or removal of infested leaves (Lyon, 1974).

Unfortunately most of the local cultivars used by farmers proved susceptible to CGM and therefore time was needed to elaborate a programme on selection and breeding of resistant cultivars. Indigenous insect predators associated with CGM were monitored but none were as diverse or as abundant as the mite family Phytoseiidae (Anon, 1985), especially at low host density. Biological control was therefore considered as a possible solution, given the fact that CGM was an introduced pest from the Neotropics (Yaninek & Herren, 1988). In the Neotropics, CGM has not been a serious pest where cassava is grown under traditional cropping systems, because adapted cultivars and natural enemies combined to suppress potential mite damage (Nyiira, 1976; Bellotti et al., 1985a, 1985b). A wide range of natural enemies have been found associated with mites in the Neotropics and surveys for further natural enemies are under

way there (Yaninek & Herren, 1988). Other common natural enemies of this mite are in the families Chrysopidae, Cecidomyidae, Syrphidae, Anthocoridae, Lygaeidae, Staphylinidae and Coccinellidae (Yaseen, 1977; Bryne et al., 1983; Murphy, 1984).

The International Institute of Tropical Agriculture (IITA) began the Africa Wide Biological Control Project (ABCP) in 1980 to control exotic cassava pests such as the cassava mealybug P. manihoti and CGM (Yaninek & Herren, 1988). Two species of phytoseiids from Columbia, namely (Neoseiulus idaeus Demark & Muma and N. anonymus (Chant & Baker), were introduced into Nigeria for mass rearing and mass release trials in 1984. To-date the following seven species of phytoseiids are being maintained under the programme: N. idaeus, N. anonymus, Galendromus annectens De Leon, Euseius concordis (Chant), Amblyseius limonicus Garman, Neoseiulus chilensis Dosse and Amblyseius aerialis Berlese. Phytoseiid predators are considered more desirable than other predators because they are more specific and survive better at low mite populations (Huffaker et al., 1970).

Initial experimental releases of N. idaeus and N. anonymus in Nigeria in 1984 and the follow-up surveys indicated that these predators dispersed slowly over a period of a few months and then disappeared (Anon, 1985). Although quite a lot is known about the long range dispersal of tetranychid mites and their phytoseiid predators (Kennedy & Smitley, 1985; Sabelis & Dicke, 1985), less is known regarding distribution and movement of CGM and its predator at the plant level.

The present investigation attempted to study the distribution and dispersal behaviour of CGM within the cassava plant and to relate this to that of its phytoseiid predators N. idaeus. Such knowledge would be helpful in planning release strategies of CGM phytoseiids in biological

SECTION 2. LITERATURE REVIEW

control programmes currently being undertaken in Africa.

The main objectives of the investigations were to determine:-

1. Which CGM stage emigrated and what leaf conditions stimulated this movement.
2. The rate of dispersal of each CGM stage under different conditions of the leaf.
3. The distribution behaviour of all stages on cassava leaves.
4. To study movement and distribution behaviour of adult CGM females within a cassava plant.
5. Which phytoseiid stage emigrated and the condition prompting such movement.
6. The searching behaviour of phytoseiids at various starvation categories.
7. Movement and distribution of Neoseiulus idaeus within the plant when prey are present.

SECTION 2

LITERATURE REVIEW

2.1 Taxonomy

The cassava green mite M. tanajoa (Bondar) sensu lato was first placed in the genus Tetranychus (Bondar, 1938), and subsequently moved to the genus Mononychellus (Wainstern, 1971). Although some researchers have considered M. tanajoa to be a synonym of M. caribbeanae (McGregor), this has not been generally accepted by other tetranychid taxonomists.

Doreste (1981) split M. tanajoa into three species, M. tanajoa, M. progresivus Doreste and M. manihot (Doreste). Such a division led some workers to report the presence of both M. tanajoa and M. progresivus in Africa (Flechtmann, 1982), but the presence of the two species in Africa has been questioned and Yaninek & Herren (1988) have suggested that the cassava green mite in Africa should be referred to as M. tanajoa (Bondar) sensu lato until and unless distinct species differences can be demonstrated.

2.2 Biology of Tetranychid mites

The life history of M. tanajoa has been studied by a number of workers (Yaseen & Bennett, 1977; Nyiira, 1975, 1978; Muaka Moko, 1981; Ezulike, 1988). It is typical of many tetranychids, in which reproduction is arrhenotokous, with the fertilized ova developing into females and unfertilized ones developing into males; it includes an egg stage and four active stages, viz. the larva, the protonymph, the deutonymph and the adult.

2.2.1 Larva: This is six legged and small in size, measuring 0.32x0.21 mm (Ezulike, 1988). It ranges from translucent white to whitish brown in colour, changing to light brown after feeding.

2.2.2 Protonymph: This is larger than the larva, has eight legs, and measures 0.42x0.29 mm (Ezulike, 1988). It is pale brown before feeding to light green in colour after feeding.

2.2.3 Deutonymph: This is similar to the protonymph except that it is larger, measuring approximately 0.53x0.42 mm and is pale brown to light green in colour (Ezulike, 1988). Ezulike (1988) also noted the sexes could be easily distinguished at this stage. The female deutonymphs are sturdy, resembling an adult female except that the legs are shorter. In addition, the abdomen of the female deutonymph is rounded whilst that of the male is pointed.

2.2.4 Adult female: Adult females are larger than the male, measuring 0.61x0.39 mm (Ezulike, 1988), have a rounded abdomen, and the setae are pronounced at this stage; their body colour depends on the amount of feeding.

2.2.5 Adult male: These are smaller than adult females, have a pointed abdomen, and the setae are less prominent. The colour is pale brown to light green depending upon the amount of feeding. They measure about 0.51x0.28 mm (Ezulike, 1988).

2.3 Developmental periods

Studies carried out by a number of workers have given more or less similar developmental periods. The duration of egg, larva, protonymphal and deutonymphal stages were given as 3-4; 1-2; 1-2 and 2-3 days respectively (Yaseen & Bennett, 1977; Nyiira, 1975, 1978; Ezulike, 1988).

Prior to each moult, there are quiescent periods which correspond to the protochrysalis, deutochrysalis and tetrochrysalis stages. These quiescent periods may last for a day at 27°C and 55-82% r.h.

The total developmental period from egg to adult reported by various workers appears to be similar even though the work was carried out under different environmental conditions. At 26.8±2.2°C and r.h. of 82% (morning) and 55% (afternoon), Yaseen & Bennett (1977) reported a period of 11-13 days. In Uganda a period of 8-13 days was found by Nyiira (1978) when the study was conducted at 22.9±3.6°C. While in Nigeria, at a temperature range between 24 and 29°C (mean 26.5±2.5°C) and a relative humidity range between 50-73% (mean 68.7±7.7), the total developmental period was 9-11 days (mean 10.3) for females and 9-10 days (mean 9.4) for males (Ezulike, 1988).

The developmental period tended to vary with both temperature and relative humidity. This was demonstrated by Muaka Toko (1981) who reported developmental periods from egg to adult of 12.3, 8.1 and 6.9 days respectively at 22, 28 and 35°C. Other workers have reported developmental periods close to that given above (Yaninek, 1985; Yaninek & Animashaun, 1984).

The preoviposition period of CGM varies from 1-3 days (Yaseen & Bennett, 1977; Nyiira, 1978; Ezulike, 1988). The oviposition period reported by these workers appeared to differ: 8-14, 12-23 and 4-17 days respectively. This was probably due to differences in the environmental conditions under which the investigations were carried out. The life span of a CGM female is three weeks on average (Yaseen & Bennett, 1977), although a period as long as 60 was reported by Nyiira (1978).

2.4 Distribution within the host plant

Species distribution refers to the spatial dispersion of individuals within a habitat at a specified moment. Tetranychid mites have their own distribution characteristics on their host plants.

Various authors have reported on the distribution behaviour of different species of spider mites. Both host plant factors and environmental factors were considered to influence the distribution of these mites. In temperate countries for instance, infestation of orchard trees by some tetranychid mites was observed to commence from the lower portions and the centre of the trees associated with the spread of overwintering survivors, reflecting the positions of the overwintering sites (Westgard & Calvin, 1971; Herbert & Butler, 1973; Wilson et al., 1984). However, the distribution of the active stages of most tetranychid mites is determined by the age of the foliage. Changes associated with ageing, unfavourable surface hardening, drying, wax deposition or inherent changes in the nutritive composition may be involved. For instance, Watson (1964) observed that Tetranychus telarius (Linnaeus) tended to be more fecund on young than on old leaves of the host plant. This was explained by differences in the nutritive value of the young and old leaves. Differences in nutrition could also account for the differences in population densities between the young and the old leaves reported by Tanigoshi et al. (1975) for Tetranychus macdaniel (McGregor) on apple and that reported by Chandler and Corcoran (1981) of Tetranychus cinnabarinus (Boisduval).

However, other species of tetranychid mites have been observed in the lower portion of their host plants where the leaves are older. The bank grass mite Oligonychus pratensis (Banks) is an example. This was found at the bottom portion of the corn plants by Gilstrap et al. (1980),

although Archer & Bynum (1986) reported it near the bottom of plants which had few leaves and nearer the middle of those which had many leaves. This shift in the distribution led the authors to suggest that the number of leaves on the corn plants influenced the mites distribution. However they did not elaborate on how the difference in the number of leaves, as characterized by varieties, influenced the mite distribution.

Distribution within plants may be associated with specific sites or at random. On cotton for example, spider mites tend to colonize the main stem node leaves near the terminal, and tend to remain in this position irrespective of the phenology of the plant (Carey, 1982; Wilson et al., 1983; Mollet et al., 1984). Random distribution is also not uncommon. Although the initial infestation will start at a specific site on the plant, the distribution becomes random with time. For instance, Wilson et al. (1984) reported random distribution for T. urticae, T. turkenstani (Ugorov & Nikolski), T. pacificus (McGregor) and the silver mite Aculus cornutus (Banks) on almond trees. Similar distributions of phytophagous mites on orchard trees were reported (Westigard & Calvin, 1971; Herbert & Butler, 1973).

Other factors may also influence the distribution of mites on plants. Environmental factors such as temperature and humidity influence distribution. On grapes in the San Joaquin Valley in the USA, different species of mite were found to prefer different locations, T. pacificus being found on hot exposed positions on the vines (southern side and top of the vine), and Eotetranychus williamettei (McGregor) on the less exposed, more humid positions (Northern side of the vines or shady areas).

2.5 Distribution of Tetranychid mites on cassava

More than 200 species of arthropod pests have been recorded on cassava (Bellotti & Schoonhoven, 1978b), of which nearly 50 species were mites (Bryne et al., 1983). Of these, the economically important species are found in the genera Tetranychus, Mononychellus and Oligonychus (Bellotti & Schoonhoven, 1978a). The distribution of these species on the plant is not the same, with most Oligonychus species, such as Oligonychus biharensis (Hirst), Oligonychus peruvianus (McGregor) (Bellotti & Schoonhoven, 1978a; Byrne et al., 1983; Bellotti, 1985), tending to colonize the basal leaves of the plant. On the other hand, T. urticae colonizes both the basal leaves and the middle leaves of the plant (Pena & Waddil, 1982), and M. tanajoa and closely related species occupy mainly leaves in the upper part of the plant near the apical bud (Nyiira, 1973, 1978; Yaseen & Bennett, 1977; Pena & Waddil, 1982; Byrne et al., 1983; Bellotti, 1985; Yaninek, 1985; Ezulike, 1988). The largest number of CGM was found between the 5th and 10th leaf from the top (Yaseen & Bennett, 1977). Nyiira (1978) reported a similar leaf age range (5-8) on both 3 and 15 month old cassava. In a study in Nigeria on cv. TMS 30555, Ezulike (1988) noted CGM on a total of 30 leaves counted from the top, the greatest populations being found on the 3rd-12th from the top (however the age of the plants was not given). Some authors have indicated that CGM can occur throughout the plant (Braun et al., 1989). The more conspicuous feeding symptoms on the leaves at the upper nodes than that on the lower leaves might have led some authors to report that the distribution of CGM was confined to the upper parts of the plants.

Factors such as secondary branching, which occurred later during the growth of cassava, combined with the shift in leaf density towards the upper part of the plant as a result of defoliation, could account for the concentration of mites in the upper node leaves. Braun et al. (1989)

reported that aggregation of CGM was greater on plants without predators and on resistant varieties of cassava but that they were less aggregated on susceptible clones and on leaves arising from the lower nodes than from the higher ones.

The colonization behaviour of tetranychid species on individual leaves has been described by Pena & Waddil (1982) and Ezulike (1988). The former authors found T. urticae mainly on the middle lobe of the leaf, concentrating near the mid vein. Ezulike (1988) found the highest numbers of CGM on the lower surface rather than on the upper surface, whilst the populations on midrib, veins, lamina and leaf junction did not differ significantly, suggesting that they were distributed randomly over the leaf. At low density, CGM was found preferentially along midribs and veins (Nyiira, 1978).

Different tetranychid species may occur together on cassava plants at the same time. The habitat stratification discussed above probably constitutes a strategy to avoid severe interspecific competition, as suggested by James (1988), who considered that CGM and the two spotted mite avoided competition on cassava by colonizing different sites.

The movement of CGM within the cassava plant is less well known. In particular, the extent of upward and downward movement with reference to the site of initial introduction has yet to be determined, and the present study aimed to determine both the speed and direction of movement.

2.6 Dispersal and migration

Movement is one of the characteristic properties of animals which distinguish them from plants. Mobility can affect a population in different ways. When movement leads to individuals becoming widely

dispersed, movement is considered to be dispersal. When movement results in individuals of the population becoming closer, such mobility leads to the contraction of the population. Collective displacement occurs when movement out of a place involves the whole population (Schneider, 1962).

The term migration in insects has a long history (Williams, 1958). It has not been easy however to define the term migration (Schneider, 1962) since people in different disciplines in the study of animals tended to use the term to address movement displayed by different species of animals. Many entomologists prior to 1970 believed that migration reflected movement which was under the control of the insects and more or less in the same direction, with a return movement sometime later to more or less the former habitat.

This to and fro kind of movement was usually observed with relatively large animals such as birds or bats (Heape, 1931; Thompson, 1949; Brower, 1961; Dorst, 1963). Similarly, the same kind of movement was observed with some insect orders, particularly the Lepidoptera in which some butterflies were normally seen moving in groups seasonally (Williams, 1930, 1957, 1958). Because the life span of most insects is shorter than that of other animals, this seasonal movement made some entomologists believe that migration could be a one way movement provided that continuity and direction were under the control of the insects themselves (Nielson, 1961). Nevertheless, such a view did not replace completely the diehard concept of the to and fro movement among most entomologists, who believed that the return migration occurred when conditions returned to normal through their progeny. This was termed 're-emigration' (Allee et al., 1949).

Division of opinion among entomologists arose over the control of direction by wind transported organisms such as aphids. Aerial movement

of insects from one secondary host to another was considered as dispersal rather than migration (Davidson, 1929) or as vagrancy (Bodenheimer & Swirski, 1957), even though some of the movements covered long distances.

Kennedy (1951) considered persistant locomotion to be the main criterion distinguishing migrants from non-migrants. This received wide support from other authors who considered undistractedness and persistence also as important aspects (Corbet, 1962; Southwood, 1962; Dingle, 1972).

According to Kennedy (1961), migration involved enhanced locomotory behaviour which resulted in persistent, straightened out movement (which did not need to be any specific direction), whilst at the same time vegetative functions associated with maintenance such as growth, feeding and reproduction were inhibited. In this definition, active and passive migration have not been distinguished, processes which Williams (1957) considered as two different phenomena.

Dingle (1972) discussed various behavioural, physiological and environmental aspects associated with insect migration. He considered that migration is an environmentally modified physiological syndrome adapted for dispersal and colonization. In this context migration usually occurs early in the life of the adult insect.

During the migratory period, further development may take place, involving the reproductive components. This is the 'oogenesis' of Johnson (1969). Migration, however, may involve reproductively mature adults under certain conditions. When this occurs, reproductive processes, such as oviposition, and those responsible for the development of ova may become inhibited. Dingle (1972) gives many examples of insects which display this adaptive behaviour.

Environmental factors and factors associated with the population of the species influence the initiation of migratory behaviour. Temperature, crowding and changes in the physiology of the host plants are the most important factors prompting migratory processes.

During migration, responses to maintenance, such as feeding, are generally suppressed but become enhanced at the destination, although there are exceptions to this condition, when feeding may occur en route, such as those reported during locust migrations (Dingle, 1972).

Dispersal and migration have been seen by different people as distinct processes. Movements within the habitat that end in feeding, mating or oviposition were considered to represent dispersal (Lawson et al., 1951; Carter, 1961). In other words, dispersal was considered to be the scattering of the animals in a purely spatial sense and was a normal event in the dynamics of population (Schneider, 1962). Andrewartha and Birch (1954) tended to share this view, and considered migration as only distantly related to dispersal. However, they stressed that dispersal was an innate tendency of animals. With insects, this tendency was phased with the other activities of adult life. However in some species with restricted ability to move in the adult stage, such as the winter moth Operophtera brumata L., the newly hatched larvae are responsible for the dispersal (Dempster, 1989).

Dispersal and migratory movements are not restricted to relatively big, flying species such as butterflies, locusts or dragonflies, but are also found in small wingless arthropods as well (Dingle, 1972).

Tetranychid mites engage in locomotion that leads to the occupation of unexploited habitats or to the colonization of new habitat through ambulatory and aerial transport (Kennedy & Smitley, 1985). Once airborne, they are passive and their destination is dependent upon the

terminal velocity (Sabelis & Dicke, 1985). The movement of tetranychid mites is therefore considered in this study as dispersion in the sense the term has been discussed above.

2.7 Dispersal of Tetranychid mites

Most tetranychid mites live in habitats which are discontinuous and impermanant. Thefore the continued existence of the species rests on the ability of its members to move to unexploited habitats within the plant or to reach suitable hosts elsewhere (Mitchell, 1970).

Tetranychids are such small arthropods that their ability to walk between hosts separated by only a few metres is very limited. Nature nevertheless has endowed mites with the reproductive capacity and behaviour to ensure that some individuals reach unexploited habitats through the available dispersal mechanisms (Mitchell, 1970).

2.7.1. Within plant movement

Within plant dispersal by most tetranychid species depends on certain groups of the population emigrating from the natal leaves to unexploited leaves within the plant. Evidence for movement within the plant has been presented for T. urticae by Hussey and Parr (1963), who observed that the teneral females emigrated from the leaves on which they had developed to other leaves up the plant irrespective of the existing population density. They also noted that movement by the ovipositing females was much more restricted when the leaf conditions were good. These results showed that newly emerged females had the tendency to emigrate, whereas such a tendency was not observed in the other stages - that is by the larvae, protonymphs or deutonymphs. However, under severe deterioration of the host plant all the age groups tend to move up the plant, where they congregated forming what they called 'spinning rope'.

All groups of Panonychus citri (McGregor) were found dispersing in orange trees, with more adult females dispersing than the other stages (Tashiro, 1966).

Density is considered a major factor prompting emigration, resulting in re-distribution within the host plants. Wrensch & Young (1978) and Archer & Bynum (1986) found that mites tended to spread throughout the plant from initial colonies or patches of infestation. Similar observations were reported by Silberman (1983), Wilson et al. (1983) and Sites & Cone (1985).

It is irrefutable that mites reach unexploited hosts within the plant or elsewhere. The important question is 'How do these small animals reach such habitats'? Dispersal in mites involves both ambulatory and aerial transport (Kennedy & Smitley, 1985).

2.7.2 Walking as a means of dispersal

Most within plant movement of tetranychids involves walking. The observations made by Hussey and Parr (1963) demonstrated this type of movement. Redistribution of mites from high density spots to areas of lower density or to unexploited spots involves an ambulatory means of transport, although aerial transport may also take place, particularly in species which spin down on silk threads. Walking was found to be the main means of dispersal for T. urticae by Margolies & Kennedy (1985). This species was reported dispersing through a succession of temporarily suitable cultivated and non-cultivated crops by crawling from field margins into peanut and corn fields. Crawling may be enhanced in fields when the canopy of the host plants intertwine. Crawling over the surface of the soil can occur, but depends upon the type of soil (Hussey & Parr, 1963). However, this is probably of minor importance compared to other means of dispersal.

2.7.3 Aerial dispersal of Tetranychid mites

The aerial dispersal of tetranychid mites in the colonization of host plants both within and between fields is undoubtedly important. Spider mites have long been known to disperse by wind, among them *P. citri*, *O. punicae*, *O. ununguis* Jacobi and *Eotetranychus sexmaculatus* (Riley). These mites have been reported spinning down from the foliage on silk threads during periods of gentle breeze which break the threads, carrying the mites aloft (Fleschner *et al.*, 1956). The mites can be carried long distances by the wind after their detachment from the threads, and Coad (1931) showed that mites could be collected at nearly 10,000 feet. In her field investigations on the European red mite, Marle (1951) observed that the great majority of those that dispersed were adult females, which normally dispersed at periods of peak population in each generation.

Not all tetranychid species display this spinning down behaviour. Species such as *T. urticae* and *T. cinnabarinus* do not spin on silken threads, although they are known to disperse aerially (Boyle, 1957).

Investigations by Hussey & Parr (1963) indicated that *T. urticae* aggregated on what they called 'roping' at the periphery of the host plant when the air was still. This behaviour, however, was not associated with aerial dispersal. The two spotted mite displayed a particular dispersal behaviour in the presence of wind (Smitley & Kennedy, 1985), which involved raising the forelegs upright to assume a dispersal posture and facing into the wind when a wind speed at 1.5m sec^{-1} or above was present.

This behaviour is very similar to that reported for the predaceous mite *Amblyseius fallacis* (Garman) (Johnson & Croft, 1976). When the host plant becomes poor, these mites manifest phototactic response (Naegele, Suski

1966) which intensifies under low relative humidity and prompts them to concentrate around the periphery of the host plant, but this behaviour does not lead to aerial dispersal.

The stages reported to display these behaviour patterns were mainly the adult females and to a lesser extent the nymphs; very rarely were the larvae implicated. Males did not demonstrate this behaviour (Brandenburg & Kennedy, 1982). Other workers who reported aerial dispersal of mites include Duffey (1956), Boyle (1957), Osakabe (1967) and Hoelscher (1967).

2.7.4 Dispersal of CGM

The dispersal behaviour of CGM is very similar to that of most tetranychid mites. CGM suspends itself on silken threads as described above (Nyiira, 1978; Yaseen & Bennett, 1977; Yaninek & Herren, 1988). This behaviour occurs in still air, particularly at high densities and when the condition of the host plant is deteriorating. The mites, once suspended, drift with the breezes (Nyiira, 1978). Nwana *et al.* (1985) and Ezulike (1988) collected dispersing CGM in traps at heights ranging from 2-3.5 m , and up to 400 m away from the source of infestation (Ezulike, 1988).

The history of the rapid spread of CGM in Africa since its discovery in Uganda in the early seventies indicates that wind is unlikley to be the main dispersal agent. It is suspected that planting materials, comprising cassava stems or sticks and also the leaves (which are consumed in some parts of Africa) may be the main agents (Yaninek & Herren, 1988). The free movement of these materials will have accelerated the spread of CGM both within countries and across borders. Evidence of CGM surviving on cassava stems with unsprouted buds for as long as 60 days in a laboratory study in Nigeria (Yaninek, personal communication) supports this claim.

Phoresy has been indicated as among the ways CGM could have spread in Africa (Nyiira, 1982), but this claim has been questioned (Yaninek and Herren, 1988). Kennedy & Smitley (1985) knew of no reports of phoretic transport of tetranychid mites, but acknowledge that such transport occurs with other groups of mites.

Despite the information on CGM dispersal both in a field and between fields, little is known about their movement within the plant.

2.7.5 Biological control of CGM

Classic biological control against CGM was initiated in 1983 under the auspices of the Africa Wide Biological Control Programme (ABCP) (Herren, 1987; Megevand et al., 1987), the objectives being to employ ecologically sound, quick and permanent control solutions to the two introduced cassava pests, the cassava mealybug Phenacoccus manihoti (Mat.-Ferr.) and the cassava green mite.

In the Neotropics, the native country of CGM, many natural enemies associated with the pest have been reported. Among the more common are species in the families Chrysopidae, Cecidomyiidae, Syrphidae, Anthocoridae, Lygaeidae, Staphylinidae, Coccinellidae and Phytoseiidae (Yaseen et al., 1977; Byrne et al., 1983; Murphy, 1984).

The presence of these natural enemies, together with the adapted cassava cultivars in the traditional farming systems, combined to suppress potential damage in the Neotropics (Bellotti, 1985). The insect predators found associated with CGM tended to be more abundant when mite populations were high, but when the populations become low, most predators dispersed in search of alternative hosts (Huffaker & Van de Vrie, 1970; Yaseen & Bennett, 1977), releasing the CGM populations to become established again.

Exotic phytoseiids were selected by the ABCP as primary agents against CGM (Yaninek, 1985b), because they have long been associated with tetranychid mites, and tend to have more specific prey requirements than most insect predators; they are therefore considered superior when mite populations are low (Huffaker et al., 1970). Phytoseiid predators have a good record in the control of spider mites in many agro-ecosystems in temperate countries (Huffaker et al., 1970; McMurtry et al., 1970; McMurtry, 1982). Following explorations in the Neotropics, a number of phytoseiid predators associated with CGM have been identified (Bellotti et al., 1987), and five species are currently being cultured at IITA Cotonou-Benin Station for further study, including experimental field release.

Neoseiulus ideaus is among the first species which were received at IITA for rearing and experimental release in 1984 (Anon, 1985).

2.7.6 Brief biology of the Phytoseiidae

Phytoseiid mites have the normal four developmental stages, although Amblyseius fallacis has been reported to develop without a deutonymphal stage (Ballard, 1954). The developmental period is usually shorter than that of its tetranychid counterparts under comparable conditions, most of them taking a minimum of 6-7 days. Both temperature and food quantity and quality affect their speed of development (Huffaker et al., 1970). Quiescent periods usually occur before each moult. Phytoseiids are arrhenotokous like the Tetranychidae. The larvae of most species feed on prey, but a few have been reported not to feed during this period (McMurtry et al., 1970).

Fecundity depends on the species and environmental conditions. Egg production rates of 2-2.5 per female per day appear to be the maximum for most species, with an average of 30-50 eggs per female common in most

species. Most eggs are laid during the early part of the adult life (McMurtry et al., 1970).

N. idaeus has a developmental period (egg to adult) of about 7 days at 27°-29°C and 70-80% r.h. condition (Animashaun, personal communication). The species has been found more tolerant of low humidity than the related species N. anonymus (Chant & Baker) (Nguyen et al., 1988).

2.7.7 Distribution of Phytoseiids on the host plant

Phytoseiid predators usually stay on the lower leaf surface and have a low photokine-sis. On the leaf, they prefer areas close to the physical junctions or protective angles formed by the leaf midribs and major veins (Putman, 1962). Typhlodromus caudiglans was also found on the bark of its host (Putman & Herne, 1964); other species have been found on low herbaceous growth and in arboreal situations - Amblyseius cucumeris for instance, has been found on low growing plants, feeding on the eggs of the clover mite; its role as a predator in trees is therefore limited (Schuster & Pritchad, 1963).

Host plant variety can influence the distribution of phytoseiid predators. T. caudiglans, for example, was found to be more numerous on such apple cultivars as Spartan & McIntosh than on Delicious (Downing & Moilliet, 1967). Other plant factors which influence phytoseiid distribution include the presence of pubescence and the size of veins. Putman (1962) and Putman & Herne (1964) reported that T. caudiglans moved more on peach trees with glabrous leaves than on apple trees with hairy leaves.

The distribution of many other phytoseiids is similar to that of their prey. Hoyt (1969), for example, found that Typhlodromus

occidentalis responded rapidly to increasing densities of T. urticae, the predator being found in all areas of the tree where the prey were distributed. P. persimilis, which is a very mobile predator, was only rarely found on leaves not infested with the two spotted mite, its prey (Oatman & McMurtry, 1966). Predators that remain near and reproduce in the colonies of its prey would be more efficient at exploiting colonial prey than widely dispersed species (McMurtry, 1982).

2.7.8 Migration and dispersal of Phytoseiids

Phytoseiids associated with tetranychid mites undoubtedly disperse since their prey live in colonies or habitats that are discontinuous and transient. Two types of dispersal can be assumed to occur. Firstly, within the plant from colonies or patches where the prey have become depleted, to other colonies or patches with prey. Secondly, interplant dispersal when prey are insufficient to ensure the survival of the predators. Colonization of prey infested plants within the neighbourhood or elsewhere has to occur. With phytoseiids, a strong tendency to disperse as the prey density declines on the host plant has been reported by a number of authors (Oatman, 1965; Takafuji, 1977; Hamamura et al., 1980; Sabelis, 1981; Bernstein, 1984).

Dispersal within the plant occurs by walking in search of new prey colonies or patches elsewhere on the plant. Long range dispersal of phytoseiids usually takes place through aerial transport, the role of ambulatory dispersal being probably restricted to short distances. In situations where foliage intertwines, interplant ambulatory dispersal is possible. In a glasshouse experiment, Van de Vrie (1985) observed that P. persimilis spread 15 m in a week from the source plant along chrysanthemum beds where the plants formed a closed canopy. In addition, A. fallacis was reported by Johnson & Croft (1981) to walk from the

orchard ground cover where they had overwintered to colonize orchard trees (apple) early in the season.

Actual aerial dispersal by phytoseiids is passive, but specific behaviour leading to lift-off has been observed for some phytoseiid species, indicating that this is an active process. Johnson & Croft (1976) found that A. fallacis changed from random to directional movement towards the edge of the arena where they orientated to the airflow, eventually assuming an anteriorly raised stance down-wind, before being carried off by the airflow. However, other observations suggest that the standing posture is not essential to achieve take-off (Sabelis & Dicke, 1985).

Field investigation using sticky traps has confirmed aerial dispersal by phytoseiids and its importance in the field. Phytoseiids were collected as far as 2 m (Johnson & Croft, 1979, 1981) and 200 m from the source (Hoy et al., 1985). More females were caught than other stages.

The dispersal of N. ideaus has not been demonstrated in the field in Africa, and the initial field releases indicated that dispersal was low, with almost all recoveries being on the plants on which the original releases were made (Anon, 1985). Such results call for more behavioural studies on these predatory mites.

2.7.9 Searching behaviour of Phytoseiids

Searching capacity is one of the five main characteristics of a natural enemy that determines its effectiveness (Hussey & Huffaker, 1976). Others include: adaptability to the environmental conditions; the capacity for increase relative to that of its prey; the capacity for prey consumption, and also such inherent properties as synchronisation with

the prey, prey specificity, degree of discrimination, ability to survive prey free periods and behavioural traits that alter the predators performance in relation to its prey's or its own density or dispersion (Huffaker et al., 1971). The ability of a natural enemy to find prey even when the latter is scarce is commonly regarded as the most important attribute of an effective natural enemy (Huffaker et al., 1969).

The searching capacity has been expressed as the natural enemy's "area of discovery" which is defined as the ratio of the number of unattacked prey to the total number of prey initially presented (Rosen & Huffaker, 1983). This area is not constant but may be affected by the density of either the prey or that of the natural enemy and possibly by various other factors as well. Location of prey by phytoseiids was previously thought to be a matter of chance when the predators came into contact with their prey (Putman, 1962; Mori & Chant, 1966; Rabbinge, 1976; McMurtry et al., 1970; Jackson & Ford, 1973). It is now known that chemical cues produced by the prey may be involved in the location of prey or their colonies (Sabelis & Dicke, 1985). These substances are known as kairomones. Brown et al. (1970) defined kairomones as substances produced or acquired by one organism (the emitter) that evoke in another organism (the receiver) a behavioural or physiological response that is adaptively favourable to the receiver but not to the emitter. Previous work suggests that the chemicals involved could be contact kairomone (Hislop et al., 1978; Hislop & Prokopy, 1981; Hoy & Smilanick, 1981).

The existence of volatile kairomones that were prey specific was first demonstrated by Sabelis and Van de Baan (1983) using a Y-tube olfactometer. Both P. persimilis and T. occidentalis showed a positive response to odour from leaves infested with P. ulmi. Field evidence regarding the effectiveness of such substances in the location of prey or

colonies is not yet available. It is possible that the searching may be directional at least at the close range.

Both prey and predator density may affect the searching behaviour of an effective natural enemy. Different species nevertheless may respond differently to such factors. For example P. persimilis has been observed to respond by reducing its searching efforts at low densities by adjusting the time spent in feeding, such that it tends to feed less on each prey at high density than it does at low densities (Eveleigh & Chant, 1981). The same authors reported an area restricted post-capture searching behaviour which, for P. persimilis, was attributed to a reduction in searching speed and an increase in absolute magnitude of turns under all prey conditions, whilst with Amblyseius degenerans (Berlese) the behaviour was related to other factors, such as the predator remaining in the general vicinity of recent prey captures for long periods of time, regardless of prey conditions (Eveleigh & Chant, 1981b).

Predators emigrate more readily as the density of their prey decreases or that of the predator increases (Sabelis, 1981; Bernstein, 1984; Ryoo, 1986). Starvation has been found to have an effect on movement (Bernstein, 1983), and increases the distance moved.

The present work looks at the movement of N. idaeus at various starvation levels in relation to the searching capability of this species.

SECTION 3. EXPERIMENT 1.

WITHIN LEAF MOVEMENT AND DISTRIBUTION OF CGM.

SECTION 3

WITHIN LEAF MOVEMENT AND DISTRIBUTION OF CGM

Introduction

The immediate problem for CGM landing on a cassava plant is to find a suitable position within the plant to settle, as they require foliage of a particular age and quality. CGM usually settle on the undersurface of the leaf where they feed, lay eggs and multiply at an impressive rate (Sabelis, 1985b). This is the initiation of the mite colony.

The increase in this population leads to a gradual deterioration of the food resource, i.e. the leaf, which, if unchecked, results in the defoliation of the host plant leaf or leaves (Nachman, 1988). Emigration is the only remedy if extinction and other catastrophic events are to be avoided.

The objectives of the series of experiments below were to determine which CGM age-groups normally emigrate and what conditions prompt this dispersal; is it mite density, or leaf age and leaf conditions? The experiment also considered rate of movement under different conditions of the leaves and of the age-groups when alone or under crowded conditions, and also the distribution of each age group within the various leaves.

3.1 Emigration behaviour of CGM age-groups studied separately

Materials and Methods:

3.1.1 The plants

Two month old Odongbo cassava plants in 15 cm diameter pots were used. Odongbo is a local western Nigerian cultivar of cassava susceptible to CGM. The third fully expanded leaf from the top was used as the experimental leaf. The highest CGM densities have been reported on this leaf (Yaninek, 1985).

3.1.2 The CGM age-groups

Cohorts of three age-groups namely, females, nymphs (protonymph and deutonymph, undiscriminated) and larvae were started from eggs laid within the same 24 hour period.

Five hundred ovipositing females obtained from a screen house culture were introduced onto 5 two-month old potted plants at the rate of 100 per plant, allowed to oviposit for 24 h and then removed. The plants were then maintained in a conviron chamber at 27°C and 55-60% r.h. As each CGM age-group developed, they were used for the experiment described below.

There were four densities for each CGM age-group, i.e. - 100, 50, 25 and 5 per leaf. There were 10 replicates of each density.

3.1.3 Experimental details:

When each CGM age-group had reached the correct stage, individuals were transferred to the experimental leaf by first being placed on 15 mm diam. discs of senescing cassava leaves on wet tissue paper in petri dishes. The discs were then transferred to the experimental leaves using

forceps, and pasted onto the distal portion of the adaxial surface of the third lobe using rubber paste. The use of senescing leaves for the discs was to prompt the mites to move onto the experimental leaf as quickly as possible. The experiment was carried out on successive days, with one CGM age-group per day, in a glasshouse at 27-29°C and 40-60% r.h.

3.1.4. The Experimental design:

The experiment was in a completely randomised design, and analysed using one-way ANOVA.

3.1.5 Data collection and statistical analyses:

Twenty-four hours after settling, counts were made of the remaining mites, the number which died (i.e. their bodies appearing dried) and those which emigrated.

The number which emigrated included those recovered from other leaves as well as those which could not be accounted for on the plant; these data were analysed as percentages and therefore subjected to transformation using square root and arc-sine methods depending on the range of the data as suggested by Gomez & Gomez (1976).

3.1.6 Results

3.1.6.i Number of individuals from each CGM age-group emigrating 24 hours after introduction.

The age-groups differed in the number of emigrants from all densities except at density 5, where the groups did not differ significantly (Table 1a). At density 100 and 50, the percentage of emigrants differed in order of the age of the groups. Females had the highest percentage of emigrants whilst larvae had the lowest. At density 25 however, females and nymphs were more or less similar, both differing

significantly from the larvae ($P < 0.005$).

The number of emigrating nymphs and larvae at each density did not differ, suggesting that their emigration did not depend on density.

The emigration by the adult females, on the other hand, tended to be density dependent with the number of emigrants declining at the lower densities (Table 1a).

3.1.6.ii Number remaining on the experimental leaves at 24 hours.

As Table 1b indicates, the percentage of each age-group remaining on the experimental leaves differed at densities 100, 50 and 25, ($P < 0.005$, $P < 0.005$ and $P < 0.025$ respectively), but not at density 5. Adult females, which had the highest number of emigrants, tended to have the fewest remaining compared with the other age-groups at the same densities. Larvae, which had the lowest percentage of emigrants, had the highest number remaining at density 100, but tended to be very similar to the nymphs at lower densities.

3.1.6.iii Number dying within 24 hours.

There was not much difference between the age-groups in the number of individuals dying at each density, except at density 100 ($P \leq 0.025$). At this density, more larvae died than the other age-groups, probably due to the handling while being transferred from the culture plants to the experimental leaves. Table 1c gives the percentage of each age-group which died at the four densities.

Figs. 1a, b and c show the percentage of each age-group emigrating, remaining or dying within 24 hours from the four densities.

Table 1. Effect of density on various parameters of CGM behaviour within 24 h of introduction to a single leaf:

CGM groups	Mean % (± SE) Densities 100	50	25	5	lsd
a. Percentage emigration[1]:					
Females	34.5±1.8 aA	23.2±1.6 aAB	18.4±2.8 aBC	14.0±3.1 c	1.13
Nymphs	14.9±1.1 b	11.4±1.1 b	13.2±2.1 a	14.0±3.1	1.08
Larvae	7.0±0.7 c	7.8±0.9 c	7.2±1.0 b	8.0±3.3	1.08
lsd	(0.44)	(0.57)	(0.84)	(1.92)	
b. Percentage remaining on leaf[2]:					
Females	59.9±1.9 cB	71.0±1.9 bA	74.0±3.5 bA	78.0±3.6 aA	6.56
Nymphs	79.1±1.3 b	82.0±1.8 a	78.0±2.3 ab	76.0±4.1 a	6.45
Larvae	84.8±0.9 a	85.2±1.5 a	85.2±2.1 a	82.0±4.7 a	7.40
lsd	(0.25)	(0.28)	(0.45)	(0.72)	
c. Percentage mortality[1]:					
Females	5.6±0.6 b	5.8±0.9	7.6±1.5	8.0±3.3	1.16
Nymphs	6.0±0.7 b	6.6±1.1	8.8±1.4	10.0±3.3	1.19
Larvae	8.2±0.5 a	7.4±0.9	7.2±1.6	10.0±3.3	1.17
lsd	0.37	0.57	1.01	2.04	

Within each section, means within a column followed by the same lower case letter do not differ significantly at the 5% level.
Means within a row followed by the same capital letter do not differ significantly at the 5% level

lsd values, [1] based on square root transformed data
[2] based on arc-sine transformed data

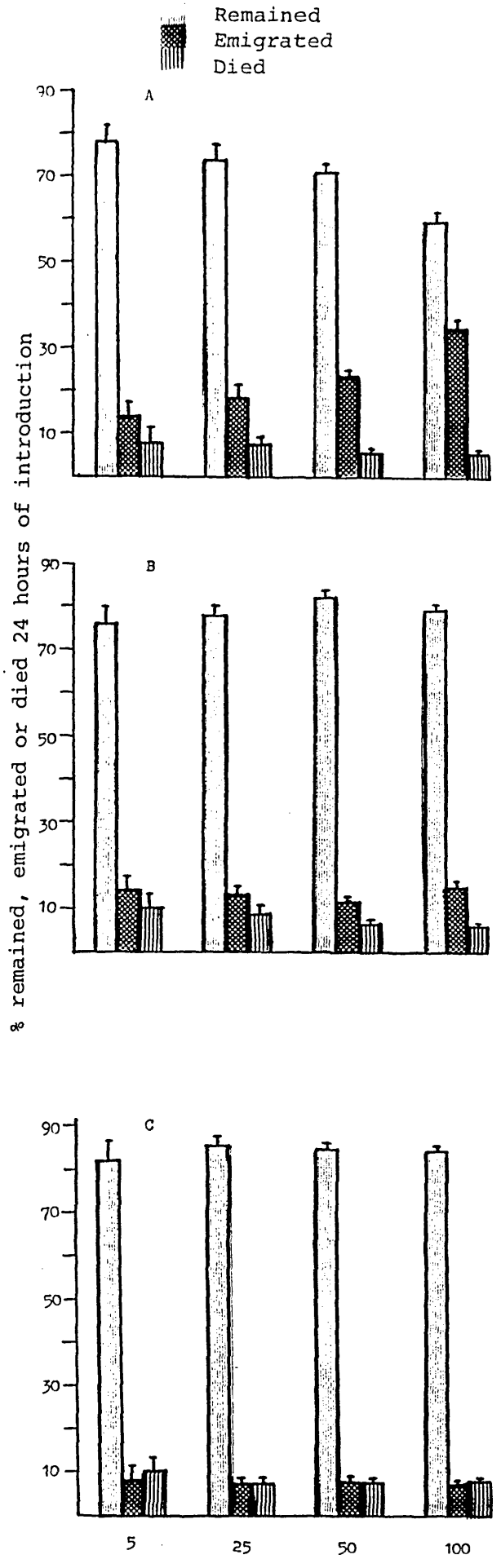


Fig. 1. Proportion of adult CGM females (A), nymphs (B) and larvae (C) which remained, emigrated and died as a percentage of the initial 100 individuals of each group introduced to the experimental leaf

3.2 Emigration behaviour monitored through the developmental periods

Materials and Methods

3.2.1 The experimental plants

The third fully expanded leaf from the top of two month old potted plants were used as the experimental leaf.

3.2.2 Initial larval populations

Cohorts were started from eggs laid over a 24 hour period as in the previous section. These were kept in a conviron chamber until they had hatched, when the larvae were placed directly onto the adaxial surface of the experimental leaf using a camel hair brush. There were 4 initial densities, i.e. 100, 50, 30 and 10 per leaf, and for each density, there were 10 replicates. The experiment was conducted in the glasshouse under the conditions shown in Table 2.

3.2.3 The trap

A piece of sellotape (Scotch type) about 4 cm long was then placed around the petiole as in Fig. 2, and Tanglefoot smeared on the sellotape without touching the petiole.

3.2.4 Daily monitoring of emigration

The sellotape on each petiole of the experimental leaf was removed carefully and immediately replaced by a new one every day. The removed sellotape trap was then stuck onto a slide and observed under a binocular microscope. The number of mites caught were recorded, and this procedure was continued until the adult stage emerged.

Table 2 Temperature and relative humidity during the developmental period from larval to the adult stage

Day	Temperature (°C) Min	Max	Relative humidity (%) Min	Max
1	20.5	30.5	53	100
2	23.0	32.5	57	100
3	24.5	32	56	97
4	22	37.5	55	99
5	22.5	32.5	50	99
6	24	37	53	100
7	24.5	36.5	51	100

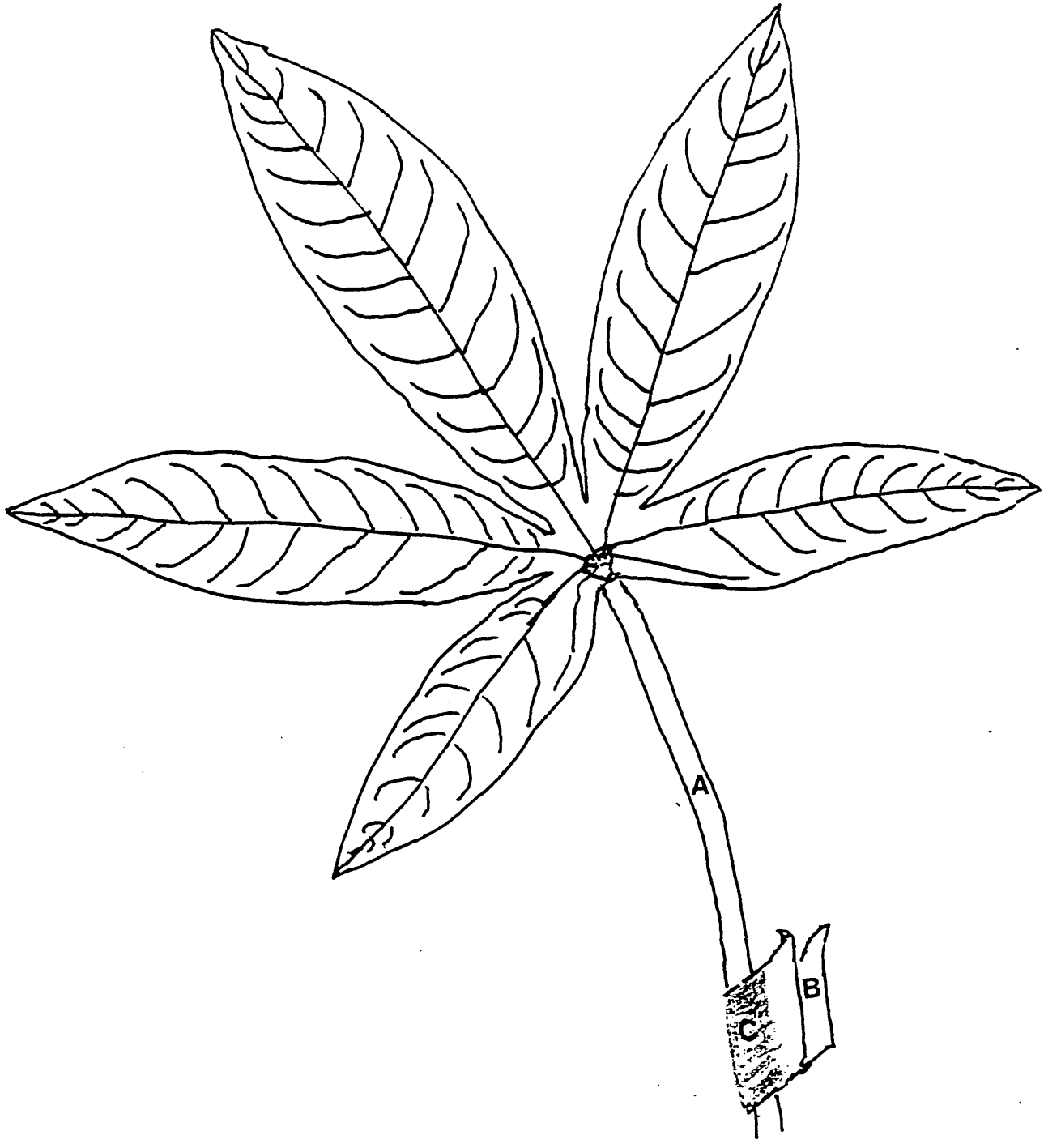


Fig. 2. Diagrammatic representation of Tanglfoot trap on the petiole of the experimental leaf. A = Petiole, B = Sellotape and C = Tanglefoot

3.2.5 Data collection and analysis

The number of mites trapped from each population density was counted daily until the adult stage emerged, when the number of adult male and female caught on the last sampling day were recorded. The numbers of individuals caught were compared between the sampling periods using one way analysis of variance, while the number of adult males and females were compared using chi-square test.

3.2.6 Results

Fig. 3 shows the trend of emigration from the larval stage through to the adult stage from four initial densities. The number of individuals caught in the traps tended to increase with each stage of development. On the first sampling day following their introduction, the mites were still in the larval stage, becoming protonymphs mainly on days two and three, whilst deutonymphs began to appear on day four and continued in this stage till the beginning of day six when adults started to emerge.

The rate of emigration, as indicated by the number caught in the traps, showed that significantly fewer larvae and protonymphs were caught ($P = 0.05$) than the other groups during the development period (Table 3) from all densities except at density 10. With the emergence of the adult stage the number caught increased even more, indicating that both adult stages had a higher tendency to emigrate than the immature groups. The number of individuals of all age groups caught in the trap at density 10 did not differ between the sampling periods suggesting that the rate of emigration did not change significantly during the developmental periods of the different groups.

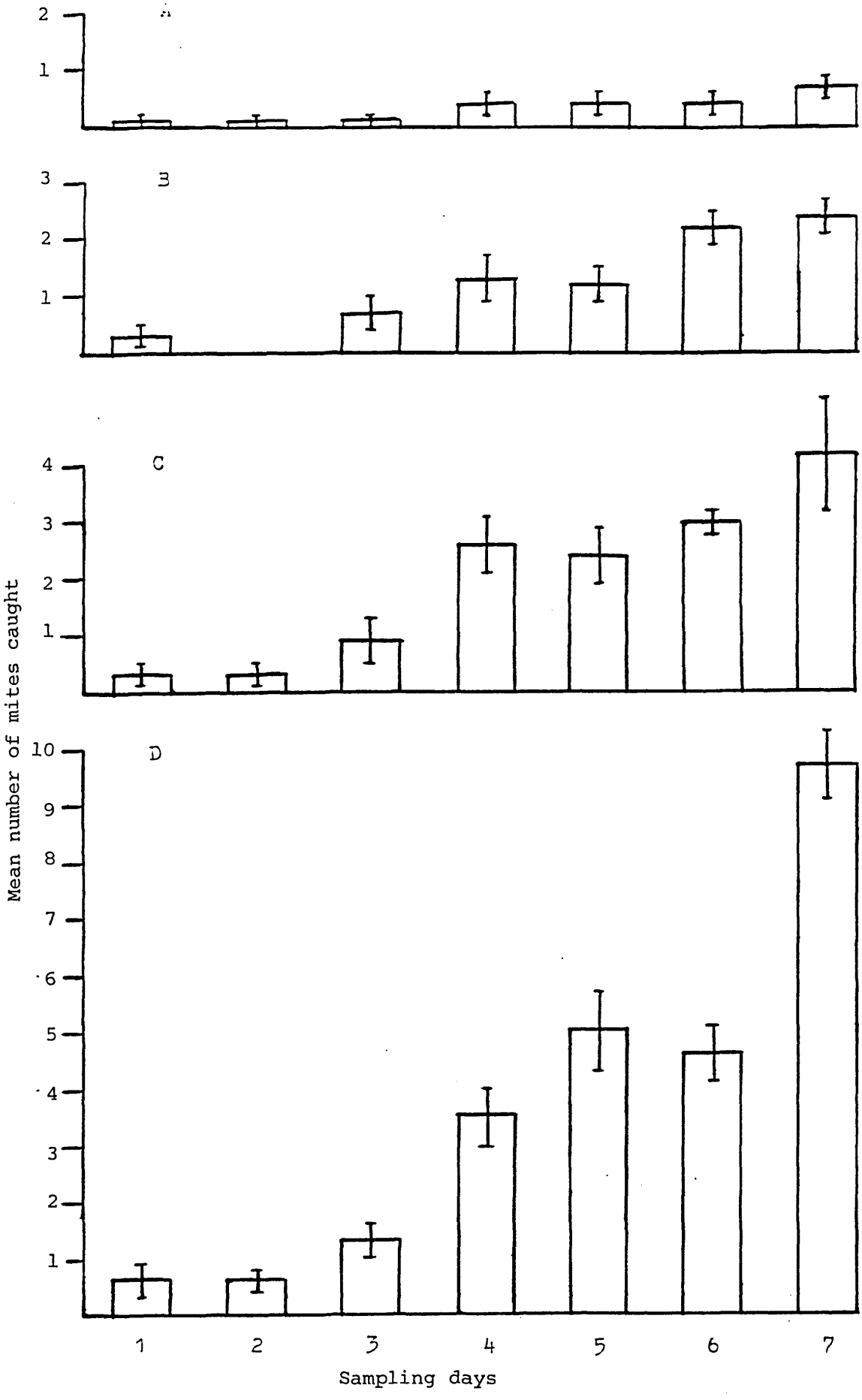


Fig. 3. Mean number of CGM caught daily in the traps from the larval to the adult stage from densities 10 (A), 30 (B), 50 (C) and 100 (D)

Table 3. Daily mean number (± SE) of individuals trapped during the developmental period at four initial population densities

Sampling days	Densities 10		30		50		100	
1	0.1±0.1		0.3±0.2	c	0.3±0.2	c	0.6±0.3	d
2	0.1±0.1		0.0		0.3±0.2	c	0.6±0.2	d
3	0.1±0.1		0.7±0.3	bc	0.9±0.4	c	1.3±0.3	d
4	0.4±0.2		1.3±0.4	b	2.6±0.5	ab	3.5±0.5	c
5	0.4±0.2		1.2±0.3	b	2.4±0.5	b	5.0±0.7	b
6	0.4±0.2		2.2±0.3	a	3.0±0.2	ab	4.6±0.5	bc
7	0.7±0.2		2.4±0.3	a	4.2±1.0	a	9.7±0.6	a
lsd 5%	(0.22)		(0.32)		(0.39)		(0.34)	

Means within a column followed by the same letter do not differ at the 5% level.
lsd values are based on square root transformed data

When the percentage of mites caught daily from larval to adult stage was compared between the densities, no significant difference was found indicating that similar percentage of individuals were emigrating daily from each density.

The mean percentage ($\pm$SE) of mites emigrating from each density were 4.72 ± 1.50, 5.67 ± 1.97, 5.18 ± 1.74 and 4.94 ± 1.98 respectively. There is little evidence to suggest that high density prompted more emigration than at low densities; in particular the proportion of females and males caught on day 7 did not differ between densities (Table 4). This similarity of emigration rate for the males compared with the females is unusual, as the presence of the females might have been expected to arrest them - perhaps competition for quiescent deutonymphs prompted their emigration.

Table 4 Comparison of number of female and male CGM emigrants trapped on the 7th sampling day at four initial population densities.

Densities	Observed Female	Male	Total	X^2 df=1 at 5%
100	46	51	97	0.26
50	18	24	42	0.86
30	9	15	24	1.5
10	2	5	7	2.25

X_2^2 values are non-significant at the 5% level.
X^2, 0.05 (df = 1) = 3.84

3.3 Movement and distribution of the different age-groups on young fully expanded cassava leaves

Materials and Methods

3.3.1 The plants

Twenty-five day old potted cassava plants, with the fully expanded third leaf from the top about 10-15 days old, were used. Prior to the start of the experiment, the shape of all the experimental leaves was outlined on paper, with the position of the veins and midrib also being noted. The area of the complete leaf and of each lobe were then calculated. Plate I shows an example of the plant used in the experiment.

3.3.2 The CGM age-groups

Cohorts of all the age-groups were used, including the adult males. These were started from eggs laid over a 24 hour period as in the previous experiments. The resulting mites were used when they had reached the correct age. Fig. 4 shows the age-groups and their developmental periods.

3.3.3 Experimental details

One hundred of each age-group were introduced separately onto the adaxial surface of the experimental leaf using a fine camel hair brush, and the plants were then transferred to a conviron chamber. There were 5 replicates per age-group and the plants were arranged in a completely randomised design.

The plants were taken from the conviron chamber to the laboratory (26-28°C and 40-55% r.h.) 6, 18 and 24 hours after the start of the experiment in order to record the positions of all mites on the



Plate 1. One month old potted Odongbo cassava plant

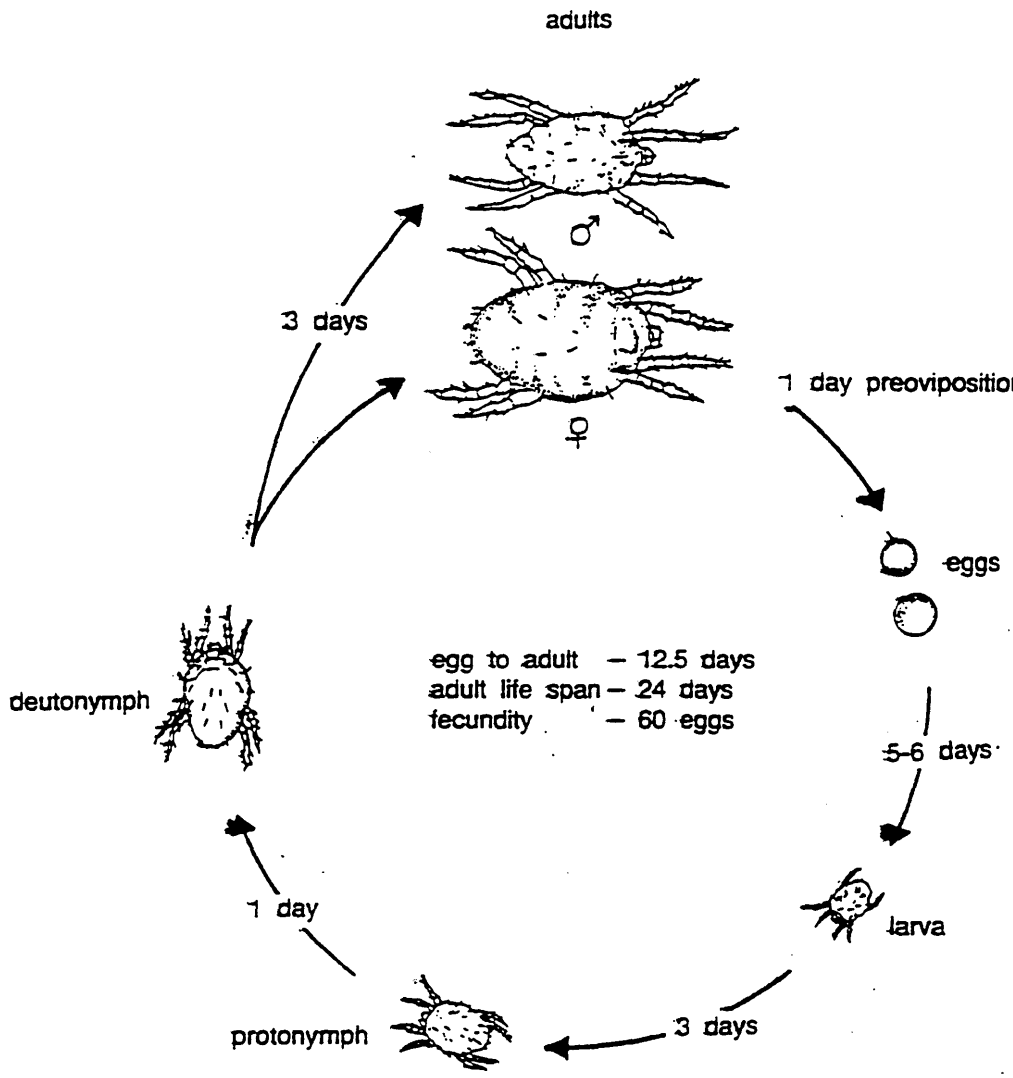


Fig. 4. Diagrammatic representation of the CGM age groups and the life cycle (After Yaninek, 1989)

experimental leaves onto photocopies of the leaves traced earlier. In order to do the recording, each experimental plant was placed on its side so that the experimental leaf could be viewed under a binocular microscope with a cold light source. This was done quickly and carefully so as to disturb the mites as little as possible. Dead mites were recorded from both surfaces at 6 hours. From these records, the distance between individuals of each age-group and the number/lobe and per leaf were determined.

3.3.4 Statistical analysis

The mean distance between individuals of each age-group was treated as a single datum for the analysis. These distances were based within each lobe rather than over an entire leaf due to the complex nature of the cassava leaf. There were 25 data for the 5 replicates.

Changes in dispersion were compared between both the time intervals and the age-groups at each time interval. Because of the rapid dispersal of the adult males, they were only included at 6 h. The density and number/lobe of all age-groups were also determined and compared between the time intervals within age-groups and between the age-groups per time interval. A split plot design was used in the analysis of the distances between individuals, density and number/lobe. One-way analysis of variance was used for the number of each age-group emigrating and for the number dying within 6 hours of introduction.

3.3.5 Results

3.3.5.i Distance between individuals, their density and the number/lobe

The distance between individuals differed between age-groups ($P<0.05$, $P<0.005$ and $P<0.05$ respectively) at 6, 18 and 24 hours (Table 5) with the males being more widely dispersed than the other groups -

Table 5 Mean distance between individuals and mean density of each CGM age-group at 6, 18 and 24 hours after introduction onto a single leaf.

CGM stage	Time (h) 6	18	24	lsd
Mean distance between individuals (mm):				
Females	6.5±0.4 b	6.6±0.5 b	6.6±0.5 a	1.21
Males	22.5±3.4 a	24.8±2.4 a	-	-
Deutonymphs	5.6±0.8 b	4.8±0.5 b	6.4±0.7 a	2.56
Protonymphs	5.1±0.4 b	4.7±0.3 b	4.4±0.3 b	1.32
Larvae	7.9±0.6 b	7.1±0.6 b	6.6±0.4 a	1.79
lsd	(1.78)	(1.77)	(0.33*)	
Mean density/cm^2:				
Females	1.3±0.10 a	1.2±0.1 a	1.2±0.1 ab	0.34
Males	0.2±0.0 cA	0.1±0.0 dB	0.1±0.0 dB	0.06
Deutonymphs	1.0±0.1 abA	1.0±0.1 bcA	0.8±0.1 cB	0.29
Protonymphs	1.3±0.1 a	1.3±0.1 a	1.3±0.1 a	0.47
Larvae	0.9±0.1 b	0.9±0.1 c	0.9±0.1 b	0.58
lsd	(0.33)	(0.29)	(0.31)	

Means within a column followed by the same letter do not differ at the 5% level

Means within a row sharing the same capital letter do not differ at the 5% level

* lsd value is based on square root transformed data

indeed so few males remained on the leaf at 24 hours that measurements of distance between individuals could not be made. The distance between individuals of the other age-groups did not differ until 24 hours, when protonymphs tended to be closer together (Table 5). After only 6 hours, more than 80% of the males had left the experimental leaves whilst only up to 14 percent of the other age-groups had left (Table 6). Table 6 also shows the percentage from each group which died within 6 hours, showing that more larvae died than the other groups except adult males.

The density and number/lobe differed between the age-groups ($P < 0.005$) at 6, 18 and 24 hours with males having the lowest density and number/lobe of all the age groups throughout the experiment (Tables 5 and 6). The density of most age-groups remained approximately constant throughout the experiment, however that of the males and the deutonymphs differed, tending to decrease with time suggesting that emigration had continued after 18 hours.

Protonymphs tended to have the greatest density and therefore the greatest number per lobe (Tables 5 and 6).

3.3.5.ii Movement and distribution of each age-group on individual leaf lobes

Tables 7 and 8 give the distance between individuals of each age-group (except males) and the number of each group remaining on each lobe respectively.

The distribution pattern and number of each age group on the individual lobes remained fairly constant throughout the experimental period. However a few lobes differed in the mean distance between individuals with time (lobe 1) for deutonymphs while the mean number of males on lobes 2, 3 and 5 suggests differences although they were not

Table 6. Mean number of each CGM age-group/lobe at 6, 18 and 24 hours after introduction, the percentage emigrants after 6 h and the mean number mortality after 6 hours.

	6h	18h	24h	lsd	% age died/leaf	% age emigrant
Females	15.8±1.1 a	15.6±1.1 b	15.0±1.1 b	2.36	4.2±0.7 b	14.4±2.8 b
Males	2.2±0.4 cA	1.4±0.2 cAB	1.0±0.2 dB	1.00	7.4±0.9 ab	81.8±2.0 a
Deutonymphs	16.2±1.9 a	15.7±1.8 b	12.2±1.2 c	2.79	5.6±1.5 b	10.4±2.2 c
Protonymphs	17.5±1.2 a	17.8±1.1 a	17.6±1.2 a	1.79	5.2±1.1 b	4.6±1.7 c
Larvae	13.3±1.1 b	14.2±1.1 b	14.1±1.0 b	2.12	11.0±1.1 a	3.8±0.3 c
lsd 5%	2.20 ?	1.60 ?	2.16		0.87[1]	6.08[2]

Means within a column followed by the same lower case letter do not differ significantly at the 5% level

Means within a row followed by the same capital letter do not differ significantly at the 5% level

1 & 2; lsd values are based on square root and arc sine transformed data respectively

Table 7 Mean distance between individuals of each age-group/lobe at 6, 18 and 24 hours after introduction.

Time interval	Mean distances (± SE) lobe 1	lobe 2	lobe 3	lobe 4	lobe 5
a. Adult females:					
6h	5.7±0.4	8.0±0.9	6.3±0.6	7.3±1.7	5.4±0.4
18h	6.0±0.6	7.2±0.9	6.3±0.9	7.8±1.9	5.9±0.4
24h	5.5±0.3	7.1±0.8	5.6±0.3	7.9±2.0	6.7±0.6
*Overall mean	5.7±0.2	7.4±0.3	6.1±0.2	7.7±0.2	6.0±0.4
b.Deutonymphs:					
6h	4.7±0.7	4.4±0.5	6.3±2.2	7.7±3.3	5.0±0.7
18h	4.6±0.9	3.4±0.6	5.2±1.8	5.8±1.3	4.6±0.6
24h	9.0±2.2	6.5±1.5	4.5±0.6	5.2±0.6	6.7±1.9
*Overall mean	6.1±1.5	4.8±0.9	5.3±0.5	6.2±0.7	5.4±0.6
c. Protonymphs:					
6h	4.3±0.5	5.1±0.6	6.2±1.5	5.8±0.8	4.0±0.7
18h	4.0±0.4	5.0±0.8	5.0±0.5	5.2±0.7	4.2±0.9
24h	4.3±0.5	4.3±0.7	4.5±0.4	4.7±0.6	2.1±1.2
*Overall mean	4.2±0.1	4.8±0.3	5.3±0.5	5.2±0.3	3.4±0.7
d. Larvae:					
6h	5.5±0.7	7.5±0.6	10.2±2.2	9.9±1.0	6.3±0.7
18h	6.0±1.4	6.0±0.5	9.8±1.6	8.7±0.6	5.1±0.4
24h	6.0±1.3	5.9±0.8	8.6±0.8	7.2±0.3	5.4±0.4
*Overall mean	5.8±0.2 b	6.4±0.5 b	9.5±0.5 a	8.6±0.8 a	5.6±0.4 b

No means within a column differed at the 5% level (Ad. females lsd = 2.88; deutonymphs lsd = 4.30; protonymphs lsd = 2.19 and larval lsd = 2.92)
Means within a row followed by the same letter or not followed by any letter do not differ at the 5% level (Adult female lsd = 1.71; deutonymph lsd = 2.32; protonymph lsd = 1.17 and larval lsd =3.93)

Table 8 Mean number (± SE) of each age-group/lobe at 6, 18 and 24 hours after introduction.

Time interval	Lobe 1	2	3	4	5
a. Adult females:					
6h	17.2±1.5	12.2±1.7	19.6±2.0	13.8±2.3	16.4±3.6
18h	15.4±1.5	14.6±2.3	19.2±3.1	15.0±3.0	13.8±2.3
24h	14.4±1.4	14.2±1.8	21.0±1.9	14.6±3.3	10.8±2.1
*Overall mean	15.6±0.8 b	13.7±0.7 b	19.9±0.6 a	14.5±0.4 b	13.7±1.6 b
b. Adult males:					
6h	1.4±0.4	2.6±0.4	3.2±1.3	0.8±0.6	2.8±1.0
18h	1.2±0.2	0.8±0.2	1.6±0.7	1.4±0.6	2.0±0.6
24h	1.0±0.5	0.4±0.2	0.8±0.2	1.8±0.7	0.8±0.2
*Overall mean	1.2±0.1	1.3±0.7	1.9±0.7	1.3±0.3	1.9±0.6
c. Deutonymphs.					
6h	14.2±4.4	14.6±3.0	21.0±7.3	15.8±3.7	15.2±1.5
18h	14.8±3.9	15.8±4.2	22.4±5.4	13.8±2.9	12.0±2.4
24h	6.2±1.4	11.0±2.8	16.8±2.1	14.2±1.6	13.0±3.1
*Overall mean	11.7±2.8 b	13.8±1.4 ab	20.1±1.7 a	14.6±0.6 ab	13.4±1.0 b
d. Protonymphs:					
6h	19.4±0.9	19.0±2.5	16.2±3.8	12.8±2.9	20.2±2.3
18h	18.4±1.0	19.2±3.1	18.4±3.7	14.6±2.2	18.4±2.4
24h	18.2±2.8	18.8±3.7	16.6±2.3	14.8±2.1	19.8±2.5
*Overall mean	18.7±0.4 ab	19.0±0.1 a	17.1±0.7 ab	14.1±0.6 b	19.5±0.6 a
e. Larvae:					
6h	15.8±3.7	12.4±1.6	11.2±2.4	9.4±0.5	17.6±1.9
18h	15.6±3.3	15.0±1.6	11.2±2.0	11.2±0.9	18.2±3.1
24h	14.6±3.5	14.8±2.1	11.4±1.4	11.4±1.0	18.4±1.9
*Overall mean	15.3±0.4 b	14.1±0.8 bc	11.3±0.1 c	10.7±0.6 c	18.1±0.2 a

Within sections of the table, no means within columns differed significantly at the 5% level (Adult female lsd = 6.73; adult male lsd = 1.70; deutonymph lsd = 10.44; protonymph lsd = 7.57 and larval lsd = 6.40)
*Means within rows sharing the same letter or not followed by any letter do not differ at the 5% level (Adult female lsd = 4.11; adult male lasd = 0.93; deutonymph lsd = 6.54; protonymph lsd = 4.77 and larval lsd = 3.93)

statistically different, possibly due to high variance in the data.

The overall mean distance between individuals differed between lobes for the larvae ($P < 0.005$) with individuals being widely distributed on lobes 3 and 4.

However the overall mean number differed between lobes for the larvae ($P < 0.005$) and for the females ($P < 0.025$) while that of the other groups did not differ.

3.4 Movement and distribution of CGM on old cassava leaves

Materials and methods

3.4.1 The plants

Two month old potted plants with the experimental leaves about 45-50 days old were used. The age of the experimental leaves were determined by tagging the first five leaves with dates as they first appeared on the sprouted cuttings. The outline of the experimental leaves was traced on paper as under Section 3.3.

3.4.2 Experimental details

The CGM age-groups used in the experiment were obtained as described under Section 3.3, and the various procedures were also similar.

3.4.3 Results

3.4.3.i CGM distribution, density and number per lobe

The CGM age-groups differed in their distribution, density and number/lobe ($P<0.005$) 6, 18 and 24 hours after introduction. The population of males was so scanty that reliable measurements of distance between individuals could not be taken. Females were the most widely distributed (Table 9), the mean distance between individuals of the other age-groups not differing throughout the experimental period.

Table 9 also compares the densities of the 5 age-groups, which differed between groups ($P<0.005$) at 6, 18 and 24 h after introduction, with the larvae having the highest density and the adults the lowest.

The lower density of the adult groups suggest that higher emigration had occurred compared with that of the immature groups. Over 80% of the

Table 9 Mean distance between individuals and mean density of each age-group at 6, 18 and 24 hours of introduction onto a single leaf.

CGM group	Time (h) 6	18	24	lsd
Mean distance between individuals (mm):				
Females	13.1±1.7 a	17.0±3.4 a	14.5±1.5 a	8.28
Deutonymphs	9.7±1.3 b	8.7±0.9 b	8.5±1.5 b	4.40
Protonymphs	5.0±0.4 c	5.5±0.5 b	4.8±0.5 b	2.18
Larvae	5.1±0.4 c	4.5±0.3 b	4.4±0.3 b	0.80
lsd	2.55	6.51	4.17	
Mean density/mites/cm^2:				
Females	0.3±0.0 dA	0.2±0.0 cB	0.2±0.0 dB	0.06
Males	0.2±0.0 d	0.1±0.0 c	0.1±0.0 d	0.14
Deutonymphs	0.8±0.1 c	0.8±0.1 b	0.7±0.1 c	0.36
Protonymphs	1.0±0.1 b	1.0±0.1 b	0.9±0.1 b	0.35
Larvae	1.4±0.2 a	1.3±0.2 a	1.4±0.2 a	0.23
lsd	(0.23)	(0.26)	(0.25)	

Means within a column followed by the same lower case letter do not differ significantly at the 5% level
Means within a row followed by the same capital letter or not followed by any capital letter do not differ significantly at the 5% level

males left within the first 6 h, the highest of all the groups. Percent emigrants from the other groups were from larvae to adult females; 4.0±1.14, 29.6±6.71, 48.2±3.93 and 67.0±1.79 and differed in order of their age group. The percentage mites which died within the first 6 hours did not differ significantly between the age groups.

The density of each age group remained fairly similar throughout the experimental period except that of females which decreased significantly after 6 hours.

3.4.3.ii Movement and distribution of CGM on leaf lobes

The distance between individuals of each CGM group on each lobe remained constant throughout the experimental period (Table 10) except that of the nymphs. Protonymphs and deutonymphs tended to be more widely distributed on the first three lobes than on the other two lobes which could be attributed to dispersal either between the lobes or away from the leaves. The numbers of mites/lobe did not appear to change after 6 h (Table 11). The overall mean number of each age-group on the five lobes did not differ significantly, except that of the protonymphs which was significantly greater on lobe 4. The number of females and males on the lobes tended to decrease with time although no significant differences were found between the three sampling periods.

Table 10 Mean distance (mm ± SE) between individuals of each CGM age-group/lobe at 6, 18 and 24 hours after introduction.

Time interval	Lobe 1	2	3	4	5
a. Adult females:					
6h	15.7±3.0	12.0±0.7	17.3±2.6	12.8±1.1	7.6±1.7
18h	9.5±1.4	17.6±5.5	14.0±4.7	22.9±13.6	21.2±8.2
24h	14.5±4.2	15.0±3.6	17.0±3.6	16.0±1.7	9.9±3.1
*Overall mean	13.2±1.9	14.8±1.6	16.1±1.6	17.2±3.0	12.9±4.2
b. Deutonymphs:					
6h	9.0±2.3	10.3±2.5	15.0±4.7	9.2±1.7	4.8±1.5
18h	8.6±2.0	9.9±2.0	10.9±2.5	8.2±1.4	5.8±1.7
24h	7.5±1.4	13.2±6.4	9.8±1.9	8.6±1.7	3.4±0.6
*Overall mean	8.4±0.5 ab	11.1±1.1 a	11.9±1.6 a	8.7±0.3 ab	4.7±0.7 b
c. Protonymphs:					
6h	5.5±0.8	5.5±1.5	5.6±1.2	5.3±0.7	3.1±0.7
18h	6.5±0.5	7.5±1.9	4.4±0.7	5.4±0.8	3.7±1.0
24h	6.3±1.0	5.6±2.2	4.6±0.8	3.4±0.5	4.0±0.9
*Overall mean	6.1±0.3 a	6.2±0.6 a	4.9±0.4 ab	4.7±0.6 ab	3.6±0.3 b
d. Larvae:					
6h	4.4±0.9	5.5±1.4	5.6±0.9	5.3±0.9	4.6±0.7
18h	4.5±1.0	4.6±0.6	5.4±0.9	4.6±0.8	3.5±0.5
24h	5.2±0.8	4.4±0.5	4.2±0.6	4.4±0.7	4.1±0.7
*Overall mean	4.7±0.2	4.8±0.3	5.1±0.5	4.8±0.3	4.1±0.3

Means within a column do not differ significantly at the 5% level (Adult female lsd = 15.25; deutonymphs lsd = 7.63; protonymphs = 3.14 and larval lsd = 2.30)

*Means within a row differ at the 5% level if they do not share the same letter (adult female lsd = 8.51; deutonymphs lsd = 4.17; protonymphs lsd = 1.55 and larval lsd = 1.40)

Table 11 Mean number of each CGM age-group/lobe at 6, 18 and 24 hours after introduction onto a single leaf.

Time interval	Lobe 1	2	3	4	5
a. Adult females:					
6h	4.0±0.5	6.8±2.2	6.8±2.5	5.8±1.3	4.8±1.6
18h	2.2±0.8	3.0±1.2	4.8±1.1	4.0±1.1	2.6±1.1
24h	2.4±0.7	1.8±0.8	4.6±0.9	4.0±1.2	2.4±1.0
*Overall mean	2.9±0.6	3.9±1.5	5.4±0.7	4.6±0.6	3.3±0.8
b. Adult males:					
6h	2.0±1.1	2.6±1.2	1.6±0.8	1.4±0.7	2.0±0.8
18h	1.4±0.7	0.4±0.2	1.0±0.8	1.8±0.7	1.2±0.6
24h	0.8±0.4	1.0±0.8	2.4±0.5	1.6±0.6	1.0±0.5
*Overall mean	1.4±0.4	1.3±0.7	1.7±0.4	1.6±0.1	1.4±0.3
c. Deutonymphs:					
6h	9.4±2.8	7.8±2.2	6.8±2.2	10.6±3.5	8.2±1.2
18h	7.2±2.4	6.6±2.2	7.0±1.4	10.8±3.5	8.8±2.5
24h	7.0±1.6	6.8±2.4	6.2±1.3	10.8±4.3	6.4±1.3
*Overall mean	7.9±1.6	7.1±0.4	6.7±0.2	10.7±0.1	7.8±0.7
d. Protonymphs:					
6h	11.0±2.7	10.2±1.1	10.2±2.1	15.6±1.7	14.8±3.7
18h	9.6±2.3	10.2±2.0	12.0±2.2	16.2±2.6	13.0±3.6
24h	7.6±2.0	12.4±2.7	11.4±1.1	18.2±2.7	9.6±2.3
*Overall mean	9.4±1.0 b	10.9±0.7 b	11.2±0.5 b	16.6±0.8 a	12.5±1.5 b
e. Larvae:					
6h	14.6±5.4	12.4±3.2	18.0±6.0	18.0±2.6	18.8±4.7
18h	11.2±4.0	16.8±4.0	19.8±6.4	18.2±3.9	13.4±3.4
24h	11.8±5.2	15.0±2.7	21.8±4.7	21.8±3.4	14.4±3.1
*Overall mean	12.5±1.1	14.7±1.3	19.9±1.1	19.3±1.2	15.5±1.7

Means within a column do not differ significantly at the 5% level (Adult female lsd = 3.71; adult male lsd = 2.08; deutonymph lsd = 7.03; protonymph lsd = 6.78 and larval lsd = 12.33)
Means within a row differ at the 5% level (lsd = 0.92) when they are not followed by a similar letter (Adult female lsd = 2.28; adult male lsd = 0.92; deutonymph lsd = 4.05, protonymph lsd = 3.72 and larval lsd = 7.82)

3.5 Movement and distribution on leaves previously damaged by CGM.

Materials and methods

3.5.1 The plants

One month old potted plants were used. The experimental leaves were exposed initially to 200 adult female CGM before the experimental CGM age-groups were introduced. The feeding damage caused by these mites was quantified by counting the number of mites that remained 24, 48 and 72 hours after introduction; the total was called mite-days. A mite-day was defined as a mite which had remained on a leaf for 24 h. The total remaining on each leaf at 24, 48 and 72 hours were therefore added to get the mite-days for each experimental leaf. The mean of the five plants (replicates) was determined, and found to be 404 mite days. From Yaninek's (1984) scale for damage, which ranges from 1-5, this is estimated to give a score of 4, at which 50% of the leaf is chlorotic. Fig. 5 shows representative symptoms on the experimental leaves used in the experiment. Seventy-two hours after introduction, all the mites and mite eggs that remained on the leaves were removed using a fine camel hair brush.

3.5.2 Experimental details

The CGM age-groups used in the experiment were obtained as described in Section 3.3, and the rest of the procedures were also similar

3.5.3 Results

3.5.3.i Distribution, density and number per lobe

As with the above results on clean and old leaves, the CGM age-groups differed in their distribution patterns 6, 18 and 24 hours after

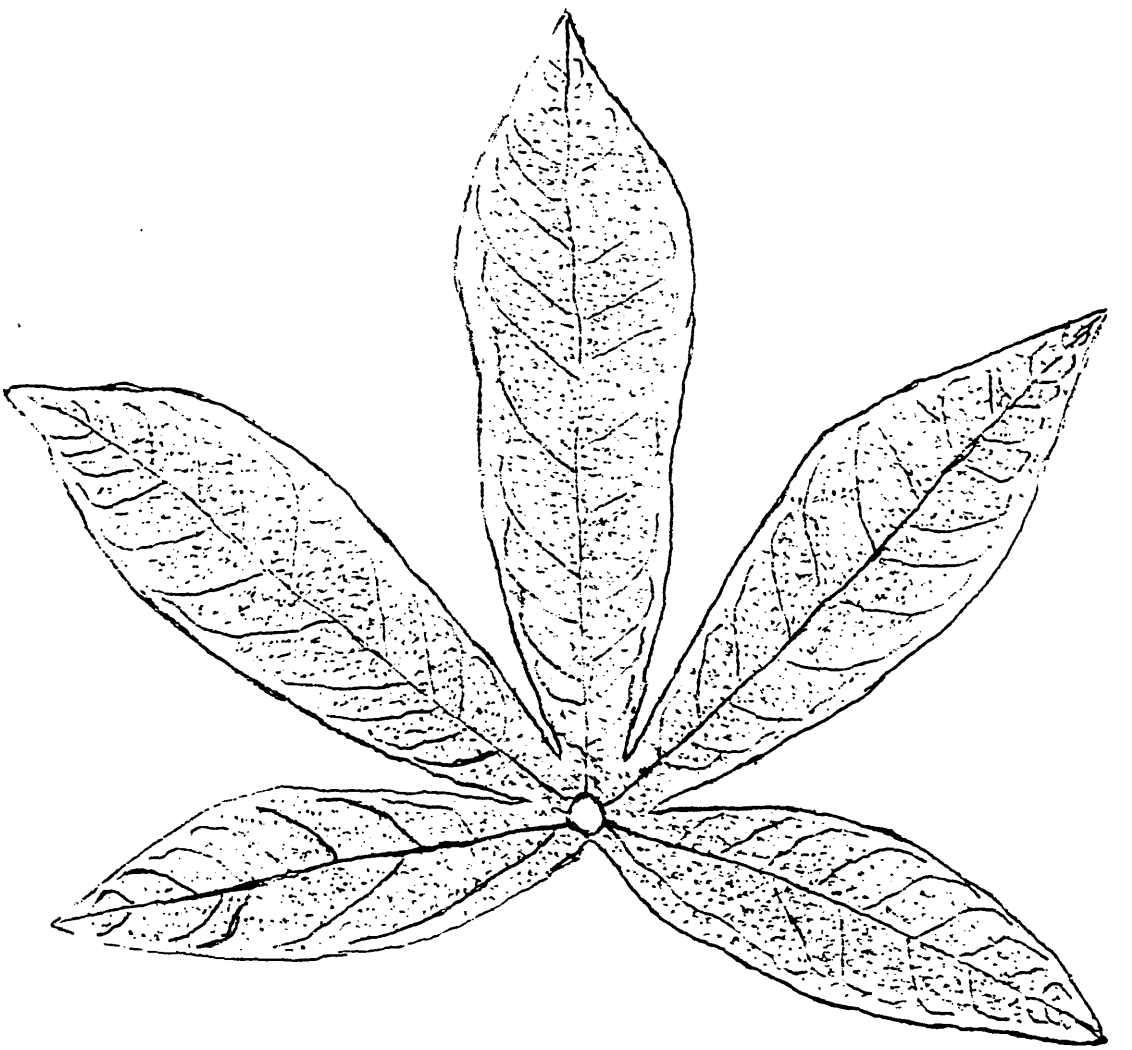


Fig. 5. Diagrammatic representation of the mite damage symptoms on experimental leaves

introduction. Both adult females and males tended to be more widely distributed than the immature age-groups throughout the experimental period, although the mean distance between individuals within each age-group remained more or less similar throughout the experimental period (Table 12), except in the males which tended to become more widely distibuted ($P \lesssim 0.05$).

Similarly, the density between the CGM age-groups and the number per lobe differed ($P \lesssim 0.005$ F, test) 6, 18 and 24 hours after introduction, although the density and number/lobe within age-groups remained fairly constant throughout the experiment. Deutonymphs, protonymphs and larvae had the highest densities and therefore the highest number per lobe (Table 12). After an initial high emigration rate during the first 6 h, both adult male and female densities and number/lobe tended to decrease significantly indicating that some emigration was still continuing. The percentage of females and males which left the leaf within the first 6 hours was greater than that of the immature groups. The percent emigrants of each group was: female 57.2±8.4; males 68.6±5.4; deutonymphs 30.0±6.4; protonymphs 31.8±1.6 and larvae 9.8±3.8. Emigration by the youngest groups after 6 h appeared to be minimal as their densities in Table 12 indicate. There were no significant differences between age groups in the percentage of individuals which died within the first 6 hours.

3.5.3.ii Distribution pattern and number of CGM per lobe

Both the distribution pattern and the number per lobe of both adult stages tended to differ between 6, 18 and 24 h on some lobes with the distance between individuals increasing during the experiment (Tables 13 and 14).

Neither the distribution pattern nor the number per lobe of any

Table 12 Mean distance (mm ±SE) between individuals and mean density of each CGM group at 6, 18 and 24 hours after introduction onto a previously mite damaged leaf.

CGM age-group	Time (h) 6	18	24	lsd
Distance between inndividuals				
Females	11.4±1.6 ab	17.1±2.5 a	19.5±2.4 a	9.41
Males	12.4±1.2 aB	18.5±2.5 aAB	19.9±1.3 aA	0.71*
Deutonymphs	5.7±0.4 c	6.0±0.4 b	5.7±0.5 b	2.19
Protonymphs	5.2±0.5 c	5.7±0.5 b	5.1±0.4 b	1.46
Larvae	7.2±0.4 c	7.1±0.6 b	6.4±0.5 b	1.16
lsd 5%	4.20	5.85	4.91	
Mean density/mites/cm^2				
Females	0.6±0.1 bA	0.3±0.04 bB	0.2±0.04 bB	0.26
Males	0.4±0.1 bA	0.2±0.03 bB	0.1±0.03 bB	0.16
Deutonymphs	1.2±0.1 a	1.2±0.1 a	1.1±0.1 a	0.28
Protonymphs	1.2±0.1 a	1.2±0.1 a	1.1±0.1 a	0.38
Larvae	1.0±0.1 a	1.1±0.1 a	1.2±0.1 a	0.44
lsd 5%	0.36	0.29	0.24	

Means within a column followed by the same lower case letters do not differ significantly at the 5% level.
Means within a row followed by the same capital letter do not differ significantly at the 5% level.
* lsd values are based on square root transformed data

Table 13 Mean distance (mm ±SE) between individuals of each age-group/lobe at 6, 18 and 24 h after introduction.

Time interval	Lobes 1	2	3	4	5
Adult females:					
6h	12.4±4.5 b	8.8±1.4	10.0±1.3 b	11.2±2.2	14.5±6.9
18h	28.7±9.8 a	12.5±1.9	16.7±5.6 ab	13.8±1.56	13.7±3.0
24h	19.7±6.7 ab	12.5±3.3	26.0±7.7 a	21.3±4.3	18.3±3.1
*Overall	20.3±4.7 A	11.3±1.2 B	17.6±4.6 AB	15.4±3.0 AB	15.5±1.4 AB
Adult males:					
6h	15.2±5.5	12.2±1.4 b	12.8±1.5	10.5±1.0	11.1±2.2 b
18h	11.5±2.6	29.0±8.1 a	13.0±3.3	19.9±5.5	19.1±4.8 ab
24h	16.3±3.1	21.5±2.9 ab	19.5±2.7	17.0±3.0	25.1±2.5 a
*Overall	14.3±1.5 B	20.9±4.9 A	15.1±2.2 AB	15.8±2.8 AB	18.4±4.4 AB
Deutonymphs:					
6h	5.5±0.7	6.4±1.1	6.8±1.1	5.5±0.7	4.5±0.6
18h	5.7±1.0	7.0±1.3	6.9±1.1	5.9±0.7	4.3±0.2
24h	6.0±1.3	6.0±0.6	6.3±1.5	5.9±1.3	4.0±0.5
*Overall	5.8±0.2 A	6.5±0.3 A	6.7±0.2 A	5.8±0.1 A	4.3±0.1 B
Protonymphs:					
6h	5.6±1.5	5.0±0.6	6.6±0.9	4.9±1.2	3.6±0.3
18h	5.3±0.6	6.2±1.4	5.7±0.9	6.5±1.5	4.6±0.7
24h	4.8±0.6	4.6±1.1	6.7±0.6	5.6±0.7	3.9±0.5
*Overall	5.3±0.2 AB	5.3±0.5 AB	6.3±0.3 A	5.7±0.5 A	4.0±0.3 B
Larvae:					
6h	6.6±0.8	7.9±0.8	8.9±0.4	7.0±0.3	5.7±0.7
18h	6.0±0.8	8.2±1.4	7.0±0.8	8.7±1.6	5.4±1.2
24h	5.7±0.4	7.2±1.7	8.6±1.5	5.7±0.8	4.6±0.6
*Overall	6.1±0.3 BC	7.8±0.3 AB	8.2±0.6 A	7.2±0.9 AB	5.2±0.3 C

Means within columns do not differ significantly at the 5% level unless followed by different letter (Adult female lsd = 13.94; adult male lesd = 10.83; deutonymph lsd = 2.80; protonymph lsd = 2.69 and larval lsd = 2.93). *Overall means followed by the same capital letter do not differ at the 5% level (Adult female lsd = 7.04; adult male lsd = 5.88; deutonymph lsd = 1.25; protonymph lsd = 1.42 and larval lsd = 1.76.)

Table 14 Mean number (±SE) of each age-group/lobe at 6, 18 and 24 hours after introduction.

Time interval	Lobes 1	2	3	4	5
Adult female:					
6h	5.8±1.3 a	7.6±1.8 a	7.8±1.1 a	7.0±1.8 a	7.4±2.2 a
18h	2.6±0.9 ab	4.2±1.7 ab	3.2±0.9 b	2.8±0.8 b	3.2±1.0 a
24h	2.0±0.5 b	3.6±1.4 b	1.4±0.5 b	1.6±0.8 b	1.2±1.0 a
*Overall	3.5±1.2	5.1±1.3	4.1±1.9	3.8±1.6	3.9±1.8
adult male:					
6h	4.6±1.1	5.6±2.0 a	4.8±1.5 a	4.6±1.2 a	4.4±1.6 a
18h	2.6±1.1	2.4±0.5 b	2.6±0.5 ab	1.6±0.24 b	2.6±0.4 ab
24h	2.0±0.7	1.0±0.5 b	1.6±0.9 b	2.0±0.9 ab	1.2±0.4 b
*Overall	3.1±0.8	3.0±1.4	3.0±1.0	2.7±0.9	2.7±0.9
Deutonymph:					
6h	11.6±1.8	12.2±1.8	13.6±2.4	14.2±2.8	11.4±1.1
18h	12.2±2.0	11.4±2.2	13.0±2.1	13.0±2.4	10.8±0.9
24h	8.0±1.3	11.4±1.6	14.8±3.0	12.0±3.1	10.6±1.0
*Overall	10.6±1.3 B	11.7±0.3 AB	13.8±0.5 A	13.1±0.6 AB	10.9±0.2 AB
Protonymph:					
6h	6.4±1.0	14.0±2.1	12.2±0.6	11.4±2.2	15.0±1.5
18h	7.2±0.7	13.2±2.4	11.4±1.7	10.8±2.3	12.4±1.9
24h	7.4±0.7	10.2±1.3	11.0±1.4	10.2±1.7	14.2±1.4
*Overall	7.0±0.3 C	12.5±1.2 AB	11.5±0.4 AB	10.8±0.4 B	13.8±0.8 A
Larvae:					
6h	15.2±4.0	11.4±1.2	8.0±1.2	13.8±0.8	18.4±3.0
18h	15.6±3.34	13.0±3.0	10.6±1.9	13.0±3.5	18.6±3.2
24h	15.2±2.6	15.0±3.1	11.2±2.1	18.6±3.5	19.8±4.0
*Overall	15.3±0.1 AB	13.1±1.0 BC	9.9±1.0 C	15.1±1.8 AB	18.93±0.44 A

Means within a column followed by the same letters do not differ significantly at the 5% level (Adult female lsd = 3.62; adult male lsd = 2.90; deutonymph lsd = 5.90; larval lsd = 8.21 & protonymph lsd = 4.60). *Overall means sharing the same capital letter do not differ significantly at the 5% level (Adult female lsd = 1.67; adult male lsd = 1.32; deutonymph lsd = 3.09; protonymph lsd = 2.71 and larval lsd = 4.72).

immature stage differed significantly during the experiment. However the overall mean distance between individuals did differ between the lobes ($\underline{P}<0.005$) for deutonymphs, ($\underline{P}<0.05$) for protonymphs and ($\underline{P}<0.01$) for larvae (Tables 13). The overall mean number on the other hand differed significantly between lobes for the protonymphs ($\underline{P}<0.005$) and for the larvae ($\underline{P}<0.01$) (Table 14).

3.6 Movement and distribution of CGM age groups on (i) leaves with slurry on proximal portions, (ii) leaves with CGM slurry on distal portion and (iii) leaves with deionized water on proximal half as control

Materials and Methods

3.6.1 The plants

Potted cassava plants as described under Section 3.3.

3.6.2 The CGM slurry

A solution was made by crushing 200 CGM females in a petri dish with 7-8 drops of deionized water. This solution was enough for treating half of the lower surface of one leaf.

Solutions were applied to the proximal half of each experimental leaf on five plants and to the distal half of each experimental leaf on a further five plants, while deionized water was applied to the proximal half of the experiment leaf on five more plants.

3.6.3 Experimental details

The experimental details were as described under Section 3.3. The treatments were carried out on successive days, completing one set of plant treatments before starting another, due to time constraints.

3.6.4 Experimental design and data analysis

The experiments were conducted in a completely randomized design. Comparisons of the mean distances between individuals of each age-group were made between the portions with and without slurry using paired t tests. No measurements were taken of the mean distance between

individuals on the distal portions of slurry treated leaves, treated on the distal portions, because most of the mites were on the untreated proximal part. The number of each age-group was similarly compared between slurry treated and untreated portion of the leaves, as well as with the deionised water treatedment.

The mean distance between individuals and the number/leaf of each age-group on each portion of the leaf were compared after 6, 18 and 24 hours, and also between the age-groups at each interval using one way analysis of variance.

3.6.5 Results

3.6.5.i Distribution patterns

Individuals in each age-group were more widely distributed on the slurry-treated proximal portions of the leaves than on the distal portions at 6, 18 and 24 h after introduction, except for the larvae at 6 and 18 h and the females at 6 hours (Table 15). On the control leaves, all age-groups except the females were denser on the water treated proximal half than on the untreated distal portions, the females becoming more widely distributed after 6 h (Table 16). These results suggest that the presence of deionized water did not deter CGM from settling.

Tables 17 shows the mean distance between individuals of each age-group 6, 18 and 24 hours on distal and proximal portions of the CGM slurry treated and the deionized water treated leaves. The distribution pattern of each age-group did not change during the period of the experiment on the residue-free distal portions of the slurry treated leaves. However, on the slurry treated proximal half, the distribution patterns of the females, deutonymphs and protonymphs differed ($P < 0.005$,

Table 15 Mean distance (mm ±SE) between individuals of each age-group on proximal and distal portions of CGM slurry treated leaves at 6, 18 and 24 hours after introduction.

CGM groups	Time (hours)	Leaf portions Distal	Proximal	T-value
Females	6h	8.3±1.0	7.0±0.6 b	0.88
	18h	9.5±0.7	19.5±1.1 a	6.91**
	24h	11.0±1.1	26.3±2.1 a	4.89**
lsd		0.27	0.25	
Deutonymphs	6h	4.8±0.3 b	9.0±1.5 b	3.37**
	18h	6.7±0.8 a	13.1±1.4 a	4.83**
	24h	7.3±0.9 a	12.5±1.5 a	2.60*
lsd		0.26	0.34	
Protonymphs	6h	5.1±0.7	8.8±0.6 b	5.93**
	18h	5.6±0.6	12.1±1.1 a	6.83**
	24h	5.8±1.0	12.5±1.8 a	6.20**
lsd		0.32	0.24	
Larvae	6h	8.6±0.6	8.2±1.1	1.07
	18h	10.2±1.4	9.1±1.5	1.27
	24h	8.3±1.8	12.5±1.6	2.31*
lsd		0.33	0.40	

*, ** Significant at 5% and 1% levels.
Within columns, data sharing the same letter or not followed by any letter do not differ at the 5% level.
t-values are based on $\log_e$ transformed data
Student's 't' and lsd values are based on $\log_e$ transformed data
t 0.05 and t 0.01, 24 df = 2.064 and 2.797 respectively

Table 16 Mean distance (mm ±SE) between individuals of each age-group on distal and proximal portions of water treated leaves at 6, 18 and 24 hours after introduction.

CGM groups	Time (hours)	Leaf portions Distal	Proximal	T-values
Females	6h	8.3±1.0	5.3±0.3 b	3.71**
	18h	7.2±0.8	6.3±0.4 ab	0.32NS
	24h	8.5±0.6	8.2±1.2 a	0.69NS
lsd		0.36	0.32	
Deutonymphs	6h	5.9±0.3	4.5±0.5	3.04**
	18h	6.8±0.6	4.3±0.3	3.77**
	24h	5.8±0.6	4.3±0.4	2.14*
lsd		0.27	0.23	
Protonymphs	6h	7.5±0.6	4.4±0.3	4.21**
	18h	7.9±0.7	4.5±0.3	4.40**
	24h	7.7±0.8	4.3±0.3	4.18**
lsd		0.36	0.20	
Larvae	6h	7.9±0.6	5.9±0.5	2.89**
	18h	8.0±0.6	5.9±0.6	2.86**
	24h	8.2±0.8	5.1±0.3	4.18**
lsd		0.30	0.25	

*, ** Significant at 5% and 1% levels.
Means within columns followed by the same letter do not differ significantly at the 5% level
Student's 't' and lsd values are based on square root transformed data
t 0.05 and t 0.01, 24 df = 2.064 and 2.797 respectively
NS = Not significant at the 5% level

Table 17 Mean distance (mm ±SE) between individuals of each group on each leaf portion of the CGM slurry and water treated leaves at 6, 18 and 24 hours after introduction.

Leaf part	CGM group	Time (hours) 6	18	24	lsd 5%
*Slurry treated leaves:					
Distal	Females	8.3±1.0 A	9.5±0.7 A	11.0±1.1 A	0.27
	Deutonymphs	4.8±0.3 B	6.7±0.8 B	7.3±0.9 B	0.31
	Protonymphs	5.1±0.7 B	5.6±0.6 B	5.8±1.0 B	0.32
	Larvae	8.6±0.6 A	10.2±1.4 A	8.3±1.8 B	0.33
lsd		0.35	0.40	0.49	
Proximal	Females	7.0±0.6 b	19.5±1.1 aA	26.3±2.1 aA	0.25
	Deutonymphs	9.0±1.5 b	13.1±1.4 aB	12.5±1.5 aB	0.30
	Protonymphs	8.8±0.6 b	12.1±1.1 aB	12.5±1.8 aB	0.24
	Larvae	8.2±1.1	9.1±1.5 C	12.5±1.6 B	0.40
lsd		0.43	0.48	0.57	
**Water treated leaves:					
Distal	Females	8.3±1.0	7.2±0.8	8.5±0.6 A	0.36
	Deutonymphs	5.9±0.3	6.8±0.6	5.8±0.6 B	0.27
	Protonymphs	7.5±0.6	7.9±0.7	7.7±0.8 A	0.36
	Larvae	7.9±0.6	8.0±0.6	8.2±0.8 A	0.30
lsd		0.33	0.32	0.33	
Proximal	Females	5.3±0.3 bAB	6.3±0.4 abA	8.2±1.2 aA	0.32
	Deutonymphs	4.5±0.5 B	4.3±0.3 B	4.3±0.4 B	0.23
	Protonymphs	4.4±0.3 B	4.5±0.3 B	4.3±0.3 B	0.20
	Larvae	5.9±0.5 A	5.9±0.6 A	5.1±0.3 B	0.25
lsd		0.22	0.23	0.30	

Means within a row followed by the same lower case letter do not differ significantly at the 5% level.
Means within a column not followed by the same capital letter differ significantly at the 5% level.
*, ** lsd values are based on $\log_e$ and square root transformed data respectively.

$P < 0.025$ and $P < 0.05$ respectively), with the mean distance between individuals of these groups increasing significantly after 6 h. The change in the observed patterns suggest either some individuals emigrated or dispersed in search of suitable site.

On the control leaves, only the distance between females differed on the proximal portion ($P < 0.025$), becoming more widely distributed at 24 hours compared with the pattern within the first 6 hours of introduction.

The mean distance between individuals differed between the age-groups throughout the experimental period ($P < 0.005$) on the slurry-free distal portion, with females and larvae tending to be more widely distributed than the nymphs (Table 17), except at 24 hour when the distribution pattern of the larvae became approximately similar to that of the nymphs.

However, on the slurry treated proximal portion, the females were more widely distributed than the immature groups but only after 6 hours of the introduction suggesting that their population was decreasing.

On the water-treated control leaves, the mean distance between individuals of each age group did not differ between the age-groups on the untreated distal portions except at 24 h when that of the deutonymphs became significantly smaller ($P < 0.025$) than that of the other groups (Table 17).

The mean distance between individuals of each group differed between the age-groups on the water treated proximal portion at 6, 18 and 24 h ($P < 0.025$; $P < 0.005$ and $P < 0.005$) respectively.

Females and larvae were distributed more widely than the other age-groups throughout the experiment except at 24 h when the mean distance between larvae decreased significantly becoming more or less similar to

that of the nymphs (Table 17). The change in the distribution pattern of the larvae suggests either some individuals had immigrated from the adaxial surface or the individuals distributed more closely later during the experiment.

3.6.5.ii Number of each age-group on slurry treated and untreated leaf portions

Adult females and the nymphs were most abundant on the slurry free distal portions throughout the experimental period except at 24 h when the population of each group became similar on both portions of the leaf (Table 18). The males on the other hand were most abundant on the slurry treated portions throughout the experimental period except at 24 h when their population became similar on both portions.

The population of larvae did not differ significantly between the slurry treated and the untreated portions throughout the experiment.

The population of each group on both the slurry treated and the untreated portions remained fairly similar throughout the experiment except that of males on the slurry free portion and females on the slurry treated portion, which decreased significantly after 6 h suggesting that some individuals had emigrated. The population of each age-group on both portions of the leaf differed between the groups throughout the experiment ($P < 0.005$).

The nymphal and larval populations were generally greater than that of the adult groups ($P = 0.05$) on the slurry free distal portions throughout the experiment. On the slurry treated proximal portions, larvae and deutonymphs were more abundant than the other groups ($P = 0.05$) throughout the experiment (Table 19).

The differences observed in the populations of the different age-

Table 18 Mean number of each age-group on distal and proximal portions of proximally slurry treated leaves at 6, 18 and 24 hours after introduction.

CGM groups	Time (hours)	Leaf portions Distal	Proximal	T-value
Female	6	15.0±1.8	8.8±0.7	3.50**
	18	11.8±1.2	5.0±1.0	4.39**
	24	9.6±1.5	5.0±0.9	3.00*
Males	6	3.4±0.6	6.2±0.7	3.00*
	18	1.8±0.8	5.8±1.6	2.31*
	24	0.8±0.4	3.0±0.8	1.92NS
Deutonymphs	6	38.6±5.2	17.4±1.6	3.75**
	18	35.2±5.6	14.6±1.9	3.34*
	24	24.8±5.0	13.4±2.5	2.02NS
Protonymphs	6	50.8±2.6	6.8±1.2	11.06**
	18	37.6±1.6	6.0±1.1	11.44**
	24	37.8±1.0	6.8±1.6	7.96**
Larvae	6	24.6±3.2	24.0±4.9	0.30NS
	18	23.2±2.4	17.6±3.9	1.51NS
	24	25.2±2.4	17.6±4.2	1.03NS

*, ** Significant at respectively 5% level and 1% level. NS = not significant at the 5% level.
Student's 't' values are based on $\log_e$+1 transformed data
t 0.05, 8 df = 2.306

Table 19 Mean number (±SE) of each age-group compared between groups on distal and proximal parts of CGM slurry treated leaves at 6, 18 and 24 hours after introduction

Leaf part	CGM group	Time (hours) 6	18	24	lsd 5%
Distal	Females	15.0±1.8 Ca	11.8±1.2 Bab	9.6±1.5 C b	0.34
	Males	3.4±0.6 Da	1.8±0.8 Cab	0.8±0.3 Db	0.77
	Deutonymphs	38.6±5.2 A	35.2±5.6 A	24.8±5.0 B	0.61
	Protonymphs	50.8±2.6 Aa	37.6±1.6 Ab	37.8±1.0 Ab	0.13
	Larvae	24.6±3.2 B	23.2±2.4 A	25.2±3.4 AB	0.37
	lsd 5%	0.37	0.56	0.47	
Proximal	Females	8.8±0.7 Ba	5.0±1.0 Bb	5.0±0.9 CDb	0.45
	Males	6.2±0.7 B	5.8±1.6 B	3.0±0.8 D	0.74
	Deutonymphs	17.4±1.6 A	14.6±1.9 A	13.4±2.5 AB	0.41
	Protonymphs	6.8±1.2 B	6.0±1.1 B	6.8±1.6 BC	0.55
	Larvae	24.0±4.9 A	17.6±3.9 A	17.6±4.3 A	0.59
		0.38	0.52	0.64	

Means within columns in each section followed by the same capital letter do not differ at the 5% level.
Means within rows in each section followed by the same lower case letter do not differ at the 5% level.
lsd values are based on $\log_e+1$ transformed data

groups on both the slurry treated proximal and the untreated distal portions throughout the experiment could be attributed to the level of tolerance each group had to the slurry treatment. Thus the lower population of the adult groups indicates more emigration and therefore lower tolerance to the slurry.

3.6.5.iii The effect of slurry treatment to the distal portion on the behaviour of CGM age-groups

Table 20 shows that the mean number of each age-group on both the distal and proximal portions of the distally slurry treated leaves 6, 18 and 24 h. The population of each age-group was highest on the slurry-free proximal portions indicating that many individuals avoided the slurry treatment on the distal portions.

The population of males decreased significantly on both portions ($P<0.005$) indicating that emigration had continued on both portions after 6 hours. On both portions, the population of each age group remained fairly constant throughout the experimental period, except that of the deutonymphs which decreased after 18 h ($P<0.025$) (Table 21) probably due to some emigration.

The population of each age-group on the slurry treated distal portions did not differ between the age-groups throughout the experiment. However on the slurry free proximal portions, the population of each age-group differed between the groups ($P<0.005$) through the experiment. Males had consistently the lowest population of all age groups throughout the experiment suggesting that the majority emigrated (Table 21).

3.6.5.iv CGM age-groups on the water treated leaves

The population of each age-group except males (18 and 24 h) was significantly greater on the water treated proximal portions than that on

Table 20 Mean number (±SE) of each age-group on the distal and proximal portions of distally slurry treated leaves 6, 18 and 24 h after introduction

CGM age groups	Time (h)	Leaf portion Distal	Proximal	T-values
Females	6	3.2±1.3	47.0±6.0	6.60**
	18	1.8±1.0	48.6±7.2	7.81**
	24	1.2±0.7	45.6±6.3	9.77**
Males	6	4.8±1.7	16.8±4.4	2.32*
	18	0.6±0.4	3.2±1.0	3.01*
	24	0.4±0.2	1.6±0.4	2.17NS
Deutonymphs	6	1.2±0.5	40.4±2.1	11.17**
	18	1.2±0.5	34.8±1.3	10.74**
	24	0.6±0.4	30.6±2.3	12.88**
Protonymphs	6	0.6±0.2	71.8±4.5	21.51**
	18	0.0	69.0±3.0	
	24	0.0	69.2±2.6	
Larvae	6	2.4±0.8	56.6±8.3	11.38**
	18	1.4±1.4	61.4±7.9	12.62**
	24	1.8±0.4	63.4±9.6	15.80**

*, ** Significant at respectively 5% and 1% level (T, 0.05, 8df = 2.306)
NS = Not significant at the 5% level
Student's 't' values are based on $\log_e$+1 transformed data

Table 21 Mean number (±SE) of each age group compared within and between groups on distal and proximal parts of distally slurry treated leaves 6, 18 and 24 h after introduction

Leaf portion	CGM age group	Time (h) 6	18	24	lsd 5%
Distal	Females	3.2±1.4	1.8±1.0	1.2±0.7	1.07
	Males	4.8±1.7 a	0.6±0.4 b	0.4±0.2 b	0.75
	Deutonymphs	1.2±0.5	1.2±0.5	0.6±0.4	0.79
	Protonymphs	0.6±0.2	0.0	0.0	
	Larvae	2.4±0.8	1.4±1.4	1.8±0.4	0.61
	lsd 5%	0.82	0.83	0.65	
Proximal	Females	47.0±6.0 AB	48.6±7.2 AB	45.6±6.3 BC	0.45
	Males	16.8±4.4 Ca	3.2±1.0 Cb	1.6±0.4 Db	0.85
	Deutonymphs	40.4±2.1 Ba	34.8±1.3 Bab	30.6±2.3 Cb	0.17
	Protonymphs	71.8±4.5 A	69.2±3.0 A	69.2±2.6 A	0.14
	Larvae	56.6±8.3 AB	61.4±7.9 A	63.3±9.6 AB	0.42
	lsd 5%	0.55	0.40	0.41	

Means within columns in each section followed by the same capital letter do not differ significantly at the 5% level
Means within rows followed by the same lower case letter do not differ significantly at the 5% level
lsd values are based on $\log_e+1$ transformed data

the untreated distal portion throughout the experiment (Table 22). The population of males on both leaf portions became fairly similar after 6 hours indicating that more emigrated from the proximal portion where the population was initially more concentrated (Table 23).

The population of the other group tended to remain fairly similar on both leaf portions throughout the experiment as Table 23 indicates.

The results generally suggest that the water did not deter most groups from settling.

Table 22 Mean number (±SE) of each age-group on the distal and proximal portions of proximally water treated leaves 6, 18 and 24 h after introduction

CGM age groups	Time (hours)	Leaf portion Distal	Proximal	T-values
Females	6	24.8±2.6	39.2±1.7	4.03**
	18	25.6±2.1	37.0±1.8	3.73**
	24	20.6±1.5	34.6±2.5	4.74**
Males	6	2.2±0.4	6.6±0.9	4.77**
	18	2.8±0.2	3.2±0.4	0.81NS
	24	1.4±0.5	2.4±0.4	1.54NS
Deutonymphs	6	17.0±2.6	58.4±3.2	8.07**
	18	19.0±2.3	53.6±3.4	7.73**
	24	16.4±2.0	52.0±3.6	7.96**
Protonymphs	6	24.4±3.0	60.2±2.1	7.30**
	18	22.6±2.2	58.0±1.7	9.80**
	24	19.6±1.9	60.0±2.0	13.79**
Larvae	6	28.8±4.6	53.0±5.0	3.30*
	18	28.0±4.2	52.2±5.4	3.22*
	24	27.4±3.9	51.6±5.8	3.22*

*, ** Significant at 5% level and 1% level respectively
Student's 't' values are based on $\log_e$+1 transformed data
t 0.05 and t 0.01, 8df = 2.306 and 3.355 respectively

Table 23 Mean number (±SE) of each age group compared within and between groups in distal and proximal parts of proximally water treated leaves at 6, 18 and 24 hours

Leaf portion	CGM age group	Time (hours) 6		18		24		lsd %
Distal	Females	24.8±2.9	AB	25.6±2.0	AB	20.6±1.5	AB	0.27
	Males	2.2±0.4	C	2.8±0.2	C	1.4±0.5	C	0.48
	Deutonymphs	17.0±2.6	B	19.0±2.3	B	16.4±2.0	B	0.40
	Protonymphs	24.4±3.0	AB	22.6±2.s	AB	19.6±1.9	AB	0.31
	Larvae	28.8±4.6	A	28.0±4.2	A	27.4±3.9	A	0.49
	lsd 5%	0.39		0.32		0.43		
Proximal	Female	39.2±1.7	B	37.0±1.8	B	34.6±2.5	B	0.18
	Males	6.6±0.9	Ca	3.2±0.4	Cb	2.4±0.4	Cb	0.37
	Deutonymphs	58.4±3.2	A	53.6±3.4	A	52.0±3.6	A	0.19
	Protonymphs	60.2±2.1	A	58.0±1.7	A	60.0±2.0	A	0.10
	Larvae	53.0±5.0	A	52.2±5.4	A	51.6±5.8	A	0.34
	lsd	0.23		0.22		0.28		

Means within columns in each section not followed by the same capital letter differ significantly at the 5% level
Means within rows in each section followed by the same lower case letter differ significantly at the 5% level
lsd values are based on $\log_e+1$ transformed data

3.6.5.v Comparison of CGM age-groups on slurry and deionized water treated leaves

Water treatment of the proximal portions of the leaves did not appear to deter the CGM age-groups from settling whilst treating the same portions with CGM slurry clearly had effect on acceptance by the different age-groups. Table 24a compares the mean number of each age-group on the proximal portions for the two treatments.

The population of each age-group with the exception of that of males was significantly greater on the water treated than that on slurry treated leaves suggesting either dispersal to the slurry free distal portions or emigration prompted by the slurry. The population of males did not differ between the proximal portions of the two treatments (Table 24a).

Females tended to be more abundant on the distal portion of the water treated than on similar portions of the slurry treated leaves. This was rather unexpected as it was deemed that more of them would migrate to the slurry free distal portions in avoidance of the slurry on the proximal parts. Probably more of the females tended to emigrate as the distal portions were similarly less favourable to them.

The protonymphs were more abundant on the distal portion of the proximally slurry treated leaves than on similar portions of the water treated leaves. However the remaining other groups did not differ between the distal portions of the two treatments in their populations (Table 24b).

These results generally suggest that there was migration from proximal slurry treated parts to the distal portions; and that similar migration from the proximal portions of the water treatment could be due

Table 24 Comparison between the mean number (±SE) of each age-group on the corresponding portions of CGM slurry and water treated leaves 6, 18 and 24 hours after introduction

CGM age group	Time (hours)	Treatment: Deionized water	Treatment: CGM slurry	T-value
(a) Proximal				
Females	6	39.2±1.7	8.8±0.7	16.50**
	18	37.0±1.8	5.0±1.0	11.40**
	24	34.6±2.5	5.0±0.9	11.08**
Males	6	6.6±0.9	6.2±0.7	0.25NS
	18	3.2±0.4	5.8±1.6	1.44NS
	24	2.4±0.4	3.0±0.8	0.44NS
Deutonymphs	6	58.4±3.2	17.4±1.6	11.16**
	18	53.6±3.4	14.6±1.9	9.51**
	24	53.0±3.6	13.4±2.5	7.20**
Protonymphs	6	60.2±2.1	6.8±1.2	12.36**
	18	58.0±1.7	6.0±1.0	14.53**
	24	60.0±2.0	6.8±1.6	10.04**
Larvae	6	53.0±5.0	24.0±4.9	3.95**
	18	52.2±5.4	17.6±3.9	5.24**
	24	51.6±5.8	17.6±4.3	4.63**

*, ** Significant at 5% and 1% level respectively (T, 0.05, 8df = 2.306) and t 0.01, 8df = 3.355. NS = not significant at the 5% level Student's 't' values are based on $\log_e$+1 transformed data

CGM age group	Time (hours)	Treatment: Deionized water	Treatment: CGM slurry	T-value
(b) Distal				
Female	6	24.8±2.6	15.0±1.8	3.10*
	18	25.6±2.1	11.8±1.2	6.03**
	24	20.6±1.5	9.6±1.5	5.07**
Male	6	2.2±0.4	3.4±0.6	1.61NS
	18	2.8±0.2	1.8±0.8	1.46NS
	24	1.4±0.5	0.8±0.4	1.27NS
Deutonymphs	6	17.0±2.3	38.6±5.2	3.46*
	18	19.0±2.3	35.2±5.6	2.30N
	24	16.4±2.0	24.8±5.0	1.37N
Protonymphs	6	24.4±3.0	50.8±2.6	5.64**
	18	22.6±2.2	37.6±1.6	5.06**
	24	19.6±1.9	37.8±1.0	6.86*
Larvae	6	28.8±4.6	24.6±3.2	0.64NS
	18	28.0±4.2	23.2±2.4	0.79NS
	24	27.4±3.9	25.2±3.4	0.36NS

*, ** Significant at 5% and 1% level respectively (T, 0.05, 8df = 2.306) and t 0.01, 8df = 3.355. NS = not significant at the 5% level Student's ' t' values are based on $\log_e$+1 transformed data

to population pressure from the proximal portions rather than the effect of water treatment.

3.6.5.vi Emigration of each age-group from the leaf treatments

The percent emigrants from each age-group differed between age-groups for all the treatments. The main dispersal occurred within the first 6 h after introduction as found more generally in the other sections above. Males had the highest percentage of emigrants in all treatments; larvae and nymphs tended to have the lowest number of emigrants. With the exception of the males, the proximally water treated leaves had the lowest percentage of emigrants of all the treatments for all the age groups (Table 25).

Table 25 Percentage emigrants from each age-group from cassava leaves with different treatments within the first 6 hours of their introduction

Treatment	Females	Males	Deutonymphs	Protonymphs	Larvae	lsd
Proximal half						
deionized water	32.0+4.3 bB	86.0+0.6 aA	19.6+1.6 cC	10.4+2.5 dC	11.6+1.5 dB	7.22
Proximal half						
CGM slurry	69.8+1.7 bA	83.6+1.7 aA	37.4+4.2 cB	33.4+2.4 cA	37.8+4.3 cA	5.52
Distal half						
CGM slurry	43.8+4.9 bB	72.2+4.2 aB	51.6+2.8 bB	20.4+4.2 cB	26.2+6.2 cA	14.05
lsd 5%	7.17	5.70	5.70	7.44	9.38	

Means within a row not followed by the same lower case letter differ significantly at the 5% level

Means within a column followed by the same capital letter do not differ significantly at the 5% level

Statistical analysis was based on arc sine transformed data

3.7 Movement and distribution of mixed age-groups on young fully expanded cassava leaves

Materials and methods

3.7.1 The plants

One month old potted plants of the same size and age as described under Section 3.3.

3.7.2 The age-groups

Cohorts of all five age-groups were used, obtained as described under Section 3.3, except that the eggs from which the cohorts were started were laid on different days, such that when eggs laid on the first day had developed to adult stage, the other batches had developed to deutonymphal, protonymphal and larval stages .

3.7.3 Experimental details

Twenty individuals of each age-group were introduced at the same time onto the experimental leaf of each experimental plant, making the total number/leaf 100. There were 5 replicates.

3.7.4 Data collection, experimental design and analysis of data

The experiment had a completely randomized design, and the methods of data collection and analysis were as described under Section 3.3.

3.7.5 Results

3.7.5.i Distance between individuals, density and number per lobe of the mixed age groups

The distance between individuals, their density and number per lobe did not differ between the sampling periods (Table 26).

The distribution pattern and the number of mites per lobe remained fairly constant throughtout the experiment (Table 27, i and ii respectively) however the overall mean distance between individuals and the mean number of the mixed groups differed between the lobes suggesting that the distribution of the individuals earlier following their release was non-random.

3.7.5.ii Distribution pattern and density of each age-group within the mixed age-group population

The distance between individuals of each age group (except males which were not included in this analysis) differed in the first 6 h ($P < 0.025$) with females being more widely distributed than the immature stages except that of the protonymphs (Table 28). The distribution pattern of each group remained fairly similar throughout the experiment.

The density of each group similarly differed between the age-groups only within the first 6 h (Table 29). Males had the lowest density of all the age-groups. However there was no suggestion that significant dispersal occurred after 6 h as the mean density of each age group remained fairly constant throughout the experiment.

Sixty-five percent of the males dispersed within the first 6 h and this was significantly greater ($P = 0.05$) than that of the other age groups.

Table 26 Comparison of mean distance between individuals of mixed age groups, density and number 6, 18 and 24 hours after introduction

Time interval	Mean distance ± SE (mm)	Mean density ± SE (mites/cm^2)	Mean number/lobe ± SE
6h	8.65±0.95	0.79±0.08	11.48±1.32
18h	9.71±2.52	0.71±0.08	10.24±1.14
24h	10.08±1.32	0.63±0.07	9.20±1.13
lsd	4.92	0.23	4.47

Means within a column do not differ signficantly at the 5% level

Table 27 Mean distance (±SE) between individuals and mean number (±SE) of mixed age-groups on leaf lobes 6, 18 and 24 h after introduction

Time interval(hours)	Lobes 1	2	3	4	5
i. Mean distance (mm):					
6	13.9±2.7	8.4±1.8	7.8±1.2	6.6±1.8	6.5±1.7
18	20.6±11.9	7.9±2.1	6.7±1.6	6.6±1.6	6.8±1.2
24	9.3±3.2	17.4±4.1	9.4±1.3	5.3±0.6	9.0±2.0
*Overall means	14.6±3.3 a	11.3±3.1 ab	8.0±0.8 b	6.2±0.4 b	7.4±0.8 b
ii. Mean number:					
6	6.8±1.7	8.6±1.2	11.8±2.3	15.8±3.3	14.4±4.2
18	6.6±1.9	7.0±1.1	10.4±2.4	15.0±3.7	12.2±1.7
24	6.2±1.8	5.4±1.2	11.0±2.5	13.0±3.0	10.4±2.8
*Overall means	6.5±0.2 b	7.0±0.9 b	11.1±0.4 a	14.6±0.8 a	12.3±1.2 a

Means within columns (i and ii) do not differ significantly (except lobe 1, section 1) at the 5% level, lsd = 10.48 and 7.5 for sections i and ii respectively

* Means within rows followed by the same letter do not differ significantly at the 5% level, lsd = 6.10 and 3.69 for section i and ii respectively

Table 28 Mean distance (mm±SE) between individuals of each age group in mixed age groups 6, 18 and 24 hours after introduction

CGM age group	Time (h) 6	18	24	lsd
Females	21.4±2.7 a	17.8±1.9	17.9±1.9	6.84
Deutonymphs	11.9±1.3 b B	12.8±1.6 B	24.1±3.3 A	10.36
Protonymphs	16.0±1.7 ab	16.6±1.9	14.4±1.8	8.15
Larvae	15.2±2.1 b	17.6±2.1	18.5±1.6	7.84
lsd 5%	5.94	8.07	9.98	

Means within a column followed by the same letter do not differ significantly at the 5% level

Means within a row followed by the same capital letter do not differ significantly at the 5% level.

Table 29 Mean density (mites/cm^2) of each age group in mixed age-groups 6, 18 and 24 h after introduction

CGM age group	Time (h) 6	18	24
Females	0.17±0.03 a	0.11±0.02	0.14±0.02
Males	0.07±0.02 b	0.08±0.01	0.08±0.02
Deutonymphs	0.17±0.03 a	0.15±0.02	0.10±0.02
Protonymphs	0.18±0.02 a	0.18±0.03	0.19±0.03
Larvae	0.20±0.03 a	0.19±0.03	0.13±0.03
lsd 5%	0.08	0.08	0.09

Means within columns followed by the same letter do not differ significantly at the 5% level

The percent emigrants from the other groups were from females to larvae; 25.0±7.4; 20.0±5.7; 17.0±4.6 and 16±6.8 respectively. There were no significant differences between age-groups in the percentage of individuals that died within the first 6 h.

3.7.5.iii Distribution pattern and population of each age-group on individual leaf lobes

The distribution pattern and the population of each age-group per lobe did not differ 6, 18 and 24 hours after introduction, suggesting that emigration after 6 h was limited (Tables 30 and 31).

The overall mean number differed between lobes for the deutonymphs ($P<0.025$), the protonymphs ($P<0.005$) and the larvae ($P<0.025$) (Table 31). The differences observed between lobes in the overall mean distance and mean number per lobe for some of the age-groups could be an indication of either some movement between the lobes or a reflection of uneven distribution of the individuals on the lobes following their release.

Table 30 Mean distance (mm±SE) between individuals of four age-groups on individual lobes 6, 18 and 24 hours after introduction.

Time interval (h)	Lobe 1	2	3	4	5
a. Adult females:					
6	23.8±5.7	16.0±3.6	23.9±9.0	19.4±2.4	12.8±3.0
18	18.6±5.2	19.3±3.4	20.1±5.4	10.4±2.5	20.7±4.1
24	15.6±1.9	20.9±2.3	24.7±6.7	15.8±4.8	12.6±2.7
*Overall mean	19.3±3.0	18.7±1.4	22.9±1.4	15.2±2.6	15.4±2.7
b. Deutonymphs:					
6	14.4±4.6	13.1±3.7	11.4±1.2	9.8±1.7	11.1±2.5
18	12.3±2.9	17.7±4.9	14.2±3.5	10.3±2.9	9.5±3.0
24	21.6±5.8	26.5±7.5	20.9±4.2	14.1±3.7	25.2±3.4
*Overall mean	16.1±2.8 b	19.1±5.8 a	15.5±2.8 b	11.4±1.4 b	15.2±5.0 b
c. Protonymphs:					
6	16.3±1.6	15.8±5.2	21.8±3.9	13.8±2.0	14.4±4.7
18	17.0±2.3	13.8±8.1	13.4±2.3	14.1±3.2	14.8±1.6
24	17.3±7.0	15.0±3.3	15.3±3.6	11.1±3.7	13.1±2.6
*Overall mean	16.9±0.3	18.2±2.8	16.9±2.6	13.0±0.7	14.1±0.5
d. Larvae:					
6	14.3±2.9	15.1±1.7	18.4±1.7	14.4±4.8	14.0±2.0
18	15.3±4.0	24.5±8.0	18.0±3.9	16.2±4.0	14.1±3.1
24	15.9±3.1	17.8±2.4	23.9±3.6	18.3±6.2	16.5±1.5
*Overall mean	15.2±0.5	19.1±2.8	20.1±1.5	16.3±1.1	14.9±0.6

Means within columns do not differ significantly at the 5% level (adult females lsd = 13.07; deutonymphs = 13.61; protonymphs = 11.59 and larvae = 13.07)

*Means within rows followed by the same letter do not differ significantly at the 5% level (adult females lsd = 7.38; deutonymphs = 6.27; protonymphs = 5.69 and larvae = 7.04).

Table 31 Mean number of each CGM age-group in mixed groups on individual lobes 6, 18 and 24 h after introduction

Time interval	Lobes 1	2	3	4	5
a. Adult females:					
6h	1.8±0.6	1.8±0.7	1.8±1.1	3.0±1.0	3.4±1.5
18h	0.8±0.4	1.0±0.8	1.8±0.7	3.2±1.6	1.6±0.6
24h	1.0±0.3	1.2±0.6	2.6±0.8	2.0±0.6	3.0±1.3
*Overall mean	1.2±0.3	1.3±0.2	2.1±0.3	2.7±0.4	2.7±0.6
b. Males:					
6h	0.6±0.6	0.8±0.4	1.0±0.6	1.0±0.3	2.4±1.5
18h	1.0±0.3	1.2±0.4	1.0±0.3	0.8±0.6	1.8±0.8
24h	0.4±0.2	1.4±0.8	1.4±0.8	1.6±0.7	1.6±0.8
*Overall mean	0.7±0.2	1.1±0.2	1.1±0.1	1.1±0.2	1.9±0.2
c. Deutonymphs:					
6h	0.8±0.4	2.2±0.9	3.0±1.5	3.2 1.0	3.0±1.2
18h	0.8±0.2	1.6±0.2	2.0±0.6	3.8±1.1	2.8±0.9
24h	0.8±0.4	1.0±0.5	2.4±1.0	3.2±1.0	1.4±0.8
*Overall mean	0.8±0.4 b	1.6±0.4 ab	2.5±0.3 a	3.1±0.5 a	2.4±0.5 a
d. Protonymphs:					
6h	1.2±0.7	2.4±0.2	3.0±0.6	4.6±1.4	2.4±0.2
18h	1.8±0.9	2.6±0.5	2.2±0.8	3.8±1.0	2.6±0.7
24h	1.4±0.4	1.2±0.2	2.8±1.2	4.6±1.2	3.0±0.6
*Overall mean	1.5±0.2 c	2.1±0.3 bc	2.7±0.2 b	4.3±0.3 a	2.7±0.2 b
e. Larvae:					
6h	2.2±1.0	1.4±0.2	2.8±0.9	4.0±1.1	3.2±0.6
18h	2.6±1.3	1.0±0.3	3.0±1.0	3.4±0.8	3.4±0.8
24h	2.4±1.0	0.6±0.2	1.6±0.9	2.2±0.7	1.6±0.7
*Overall mean	2.4±0.1 ab	1.0±0.2 b	2.5±0.4 a	3.2±0.5 a	2.7±0.6 a

Means within columns do not differ significantly at the 5% level (Adult female lsd = 0.79; male = 0.65; deutonymphs = 0.71; protonymphs = 0.63 and larvae = 0.70)
*Means within rows followed by the same letter do not differ significantly at the 5% level (adult females = 0.44; males = 0.35; deutonymphs = 0.40; protonymphs = 0.31 and larvae = 0.40)
lsd values are based on square root (+0.5) transformed data)

3.8 Within age-group distribution on cassava leaves with different treatments

3.8.i Females

The mean distance between individual females differed between the experimental leaves throughout the experimental period with individuals being more widely distributed on old leaves; previously mite damaged leaves and on leaves with CGM slurry on the proximal portions ($P = 0.05$) than on young leaves and on distally slurry treated leaves (Table 32).

The population of the adult females similarly differed between the leaf treatments as did the distribution pattern.

Young fully expanded leaves had the highest population of all the experimental leaves (Table 33). The differences in the populations observed between the leaves were due to emigration which differed probably depending on the leaf's acceptance to the mite.

3.8.ii Males

Males tended to disperse rapidly following their introduction to the leaves. Their distribution on leaves was so scanty that reasonable measurements of distance between individuals could not be made throughout the experimental period. Their distribution on the various leaves is presented on the basis of their number per lobe. The number of males that remained on the leaves following their dispersal within the first 6 h was generally low on most of the leaves. The density per lobe however was consistently greater on previously mite damaged leaves than that on other leaves (Table 33) throughout the experimental period. The high density found on these leaves was attributed to the presence of females which were initially introduced to the leaves and removed prior to the beginning of the experiment. It was possible therefore that some odour

Table 32 Mean distance between CGM age-groups on cassava leaves treated variously 6, 18 and 24 hours after introduction.

Treatment (leaves)	Mean distance (± SE) mm per lobe Time (hours) 6	18	24
a. Adult female:			
Young fully expanded	6.5±0.4 b	6.6±0.5 b	6.6±0.5 b
Old leaves	13.0±1.7 a	17.0±3.4 a	14.5±1.5 a
Previously mite damaged	11.4±1.6 a	17.1±2.5 a	19.5±2.4 a
Leaf with CGM residue proximal half	15.4±2.0 a	19.7±2.7 a	20.2±3.2 a
Leaf with CGM residue distal half	6.7±0.7 b	6.9±1.1 b	6.7±1.1 b
lsd 5% level	(4.29)	(8.25)	(5.97)
b. Deutonymphs:			
Young fully expanded	5.6±0.8 c	4.7±0.5 c	6.4±0.7 bc
Old leaves	9.7±1.3 a	8.7±0.9 ab	8.5±1.5 ab
Previously mite damaged	5.7±0.4 c	6.0±0.4 bc	5.7±0.5 c
Leaf with CGM residue proximal half	8.3±1.3 ab	8.4±0.7 ab	9.0±0.8 a
Leaf with CGM residue distal half	6.8±0.5 bc	9.2±0.9 a	8.8±0.7 ab
lsd 5% level	(2.60)	(2.87)	(2.45)
c. Protonymphs:			
Young fully expanded	5.1±0.4 b	4.7±0.3 bc	4.4±0.3 b
Old leaves	5.0±0.4 b	5.5±0.5 bc	4.8±0.5 b
Previously mite damaged	5.2±0.5 b	5.7±0.5 b	5.1±0.4 b
Leaf with CGM residue proximal half	6.8±0.7 a	9.5±1.2 a	8.7±1.0 a
Leaf with CGM residue distal half	4.4±0.2 b	3.8±0.2 c	3.6±0.2 b
lsd 5% level	(1.36)	(1.82)	(2.02)
d. Larvae:			
Young fully expanded	7.9±0.6 b	7.1±0.6 b	6.6±0.4 b
Old leaves	5.1±0.4 c	4.5±0.3 b	4.4±0.3 b
Previously mite damaged	7.2±0.4 bc	7.1±0.6 b	6.4±0.5 b
Leaf with CGM residue proximal half	10.7±0.9 a	12.4±1.3 a	13.5±1.9 a
Leaf with CGM residue distal half	6.0±0.5 bc	4.6±0.4 b	5.0±0.5 b
lsd 5% level	(2.29)	(2.55)	(2.53)

Mean for a given age-group within a column followed by the same letter(s) do not differ significantly at the 5% level

Table 33 Mean number of each age-group on cassava leaves of different treatments 6, 18 and 24 hours after introduction.

Treatment (leaves)	Mean number (± SE) per lobe Time (hours) 6	18	24
a. Adult females:			
Young fully expanded	15.8±1.1 a	15.6±1.1 a	15.0±1.1 a
Old leaves	5.6±0.8 c	3.3±0.5 c	3.0±0.4 c
Previously mite damaged	7.1±0.7 c	3.2±0.5 c	2.0±0.4 c
Leaf with CGM residue proximal half	5.0±0.5 c	3.3±0.3 c	3.0±0.3 c
Leaf with CGM residue distal half	10.1±1.0 b	10.1±1.1 b	9.3±1.1 b
lsd 5% level	(2.42)	(2.14)	(2.26)
b. Adult males:			
Young fully expanded	2.2±0.4 bc	1.4±0.2 b	1.0±0.2 bc
Old leaves	1.9±0.4 c	1.2±0.3 b	1.4±0.3 ab
Previously mite damaged	4.8±0.6 a	2.4±0.3 a	1.6±0.3 a
Leaf with CGM residue proximal half	1.9±0.2 c	1.5±0.3 ab	0.7±0.2 bc
Leaf with CGM residue distal half	4.3±0.6 ab	0.8±0.2 b	0.4±0.1 c
lsd 5% level	(2.31)	(0.88)	(0.76)
c. Deutonymphs:			
Young fully expanded	16.2±1.9 a	15.8±1.8 a	12.2±1.2 a
Old leaves	8.6±1.1 c	8.1±1.1 cd	7.4±1.1 b
Previously mite damaged	12.6±0.9 b	12.1±0.8 b	11.4±1.0 a
Leaf with CGM residue proximal half	11.2±1.1 bc	9.8±0.8 bc	7.9±0.9 b
Leaf with CGM residue distal half	8.4±0.8 c	7.2±0.8 d	6.2±0.7 b
lsd 5% level	(2.85)	(2.53)	(3.32)

Table 33 (cont.)

Treatment (leaves)	Mean number (+ SE) per lobe Time (hours) 6	18	24
d. Protonymphs:			
Young fully expanded	17.5±1.2 a	17.8±1.1 a	17.6±1.2 a
Old leaves	12.4±1.1 bc	12.2±1.2 bc	11.8±1.2 c
Previously mite damaged	11.8±0.9 c	11.0±0.9 cd	10.6±0.7 cd
Leaf with CGM residue proximal half	11.6±1.6 c	8.8±1.2 d	8.9±1.2 d
Leaf with CGM residue distal half	14.4±1.0 b	13.8±0.7 b	14.0±0.7 b
lsd 5% level	(2.24)	(2.37)	(2.13)
e. Larvae:			
Young fully expanded	13.3±1.1 ab	14.3±1.1 ab	14.1±1.0 ab
Old leaves	16.4±1.9 a	15.9±1.9 a	17.0±1.8 a
Previously mite damaged	13.4±1.2 ab	14.2±1.4 ab	16.0±1.4 ab
Leaf with CGM residue proximal half	9.6±1.1 c	8.5±1.0 c	8.6±1.1 c
Leaf with CGM residue distal half	11.8±1.5 bc	12.5±1.2 b	13.0±1.3 b
lsd 5% level	(3.69)	(3.14)	(3.33)

Means for a given age-group within a column not followed by the same letter differ significantly at the 5% level

or pheromone ilicited by their feeding might have played a role in the arrestment of these males.

The presence of crushed slurry on either the proximal or distal portions of leaves appeared to have less attraction to the males. It was probable however that the presence of the CGM slurry confused the males early during the experiment as the density on the leaves with the smear on the distal portions indicates. The good condition of leaves did not appear to encourage males to settle indicating that feeding was not the priority for them.

3.8.iii Deutonymphs

The distribution of this age-group on each leaf differed between the leaf treatments 6, 18 and 24 h ($P<0.01$, $P<0.025$ and $P<0.025$ respectively) (Table 32). Individuals distributed more closely on young fully expanded leaves and on previously mite damaged leaves than on the other leaves.

The number per leaf similarly was greater on leaves the deutonymphs were more closely distributed than on the other leaves on which they were widely distributed (Table 32). Good condition of the leaves appeared to attract more individuals to settle. Similarly previously mite damaged leaves attracted more mites probably because they are so close to the condition in which this age-group and the other immature age-groups develop.

3.8.iv Protonymphs

As the mean distance between individuals indicates (Table 32) the distribution patterns differed between the leaves ($P<0.05$, $P<0.005$ and $P<0.005$ respectively) 6, 18 and 24 h. Individuals however tended to be more closely distributed on all the leaves except on leaves with CGM

slurry on the proximal portions of the leaves. The density per lobe similarly followed closely the distribution patterns with lowest density found on the leaves with the slurry on the proximal portions (Table 33). Young fully developed leaves tended to have significantly greater number of individuals than the rest of the leaves. The low density on leaves with the slurry on the proximal portions suggests that more individuals left the leaves due to both the presence of the slurry and that the proximal portions with the slurry are probably more preferable to the distal portions. The presence of the slurry on the proximal portions should have encouraged more individuals to settle on the distal portions free of the CGM slurry.

3.8.v Larvae

The distribution patterns of this age-group on the various leaves followed closely that of the protonymphs. The distribution patterns differed between the various leaves ($P<0.005$) respectively 6, 18 and 24 h (Table 31). The number of larvae which remained on the leaves similarly differed ($P<0.01$, $P<0.005$ and $P<0.005$) respectively at 6, 18 and 24 h (Table 32).

The mean distance between individuals indicates that the larvae were more widely distributed on leaves which had CGM slurry on the proximal portions than that on the rest of the leaves. The same leaves on which the larvae were more widely distributed tended to have the lowest population.

Surprisingly old leaves tended to have the highest number of larvae of all the leaf treatments, appearing to suggest that old leaves were the most favourable leaves. However their abundance on these leaves could be coincidental, reflecting the low tendency for them to disperse. The larvae probably do not require much food during their development to the

next stage and therefore leaf quality is not as critical as it is for the other age-groups.

3.9 Results

3.9.i The distribution of each CGM age-group on the palm, middle and distal sections of cassava leaves of different treatments

The distribution behaviour of the CGM age-groups from the petiole junction to the distal end of the various experimental leaves tended to be similar.

The palm section tended to have the highest density of each age group on the various leaves throughout the experimental period except for few cases in which the distribution was similar on all the sections (Tables 34, 36 and 38).

However adult females and males on young fully expanded leaves and males on old leaves tended to have a similar distribution on all the leaf sections at 24 h (Tables 34 and 36) probably due to some emigration.

In Figs. 6, 7 and 8 the distribution of adult females on the leaf sections at 6, 18 and 24 hours on young fully expanded, old and mite damaged leaves respectively is given.

The population of each group on each leaf section of most experimental leaves remained relatively similar throughout the experiment. However on some of the leaf sections the population of some CGM groups appeared to decrease with time. For instance the densities of females and deutonymphs on the palm and that of males on the middle sections of young fully expanded leaves decreased significantly at 24 h (Table 35, $\underline{P} = 0.05$). The change in the population of these groups suggests that either migration to the other leaf sections or emigration from the leaf had occurred.

On old leaves the population of females on both the middle and

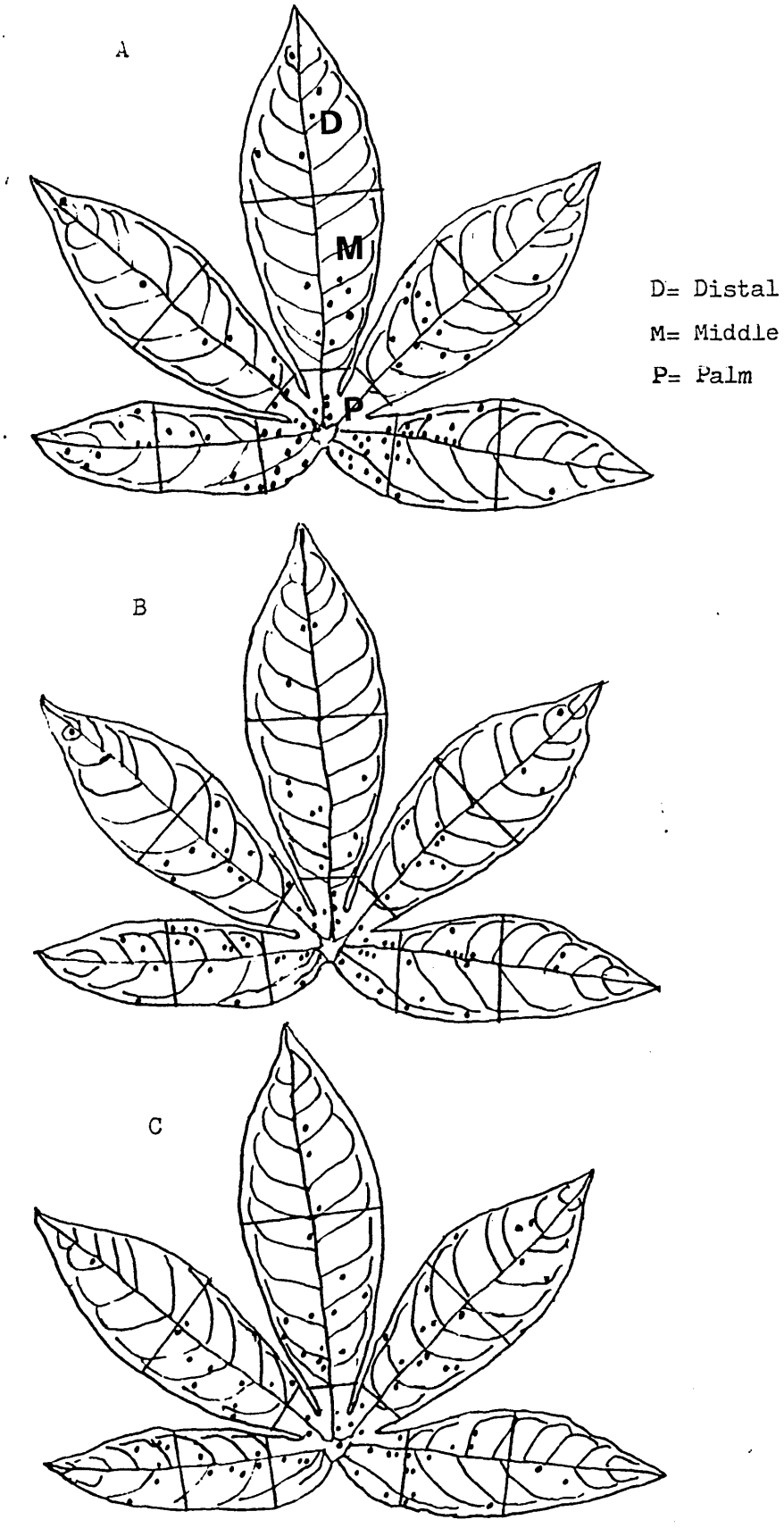


Fig. 6. Distribution of female CGM on palm, middle and distal section of young fully expanded leaf at 6 (A), 18 (B) and 24 (C) hours after the introduction

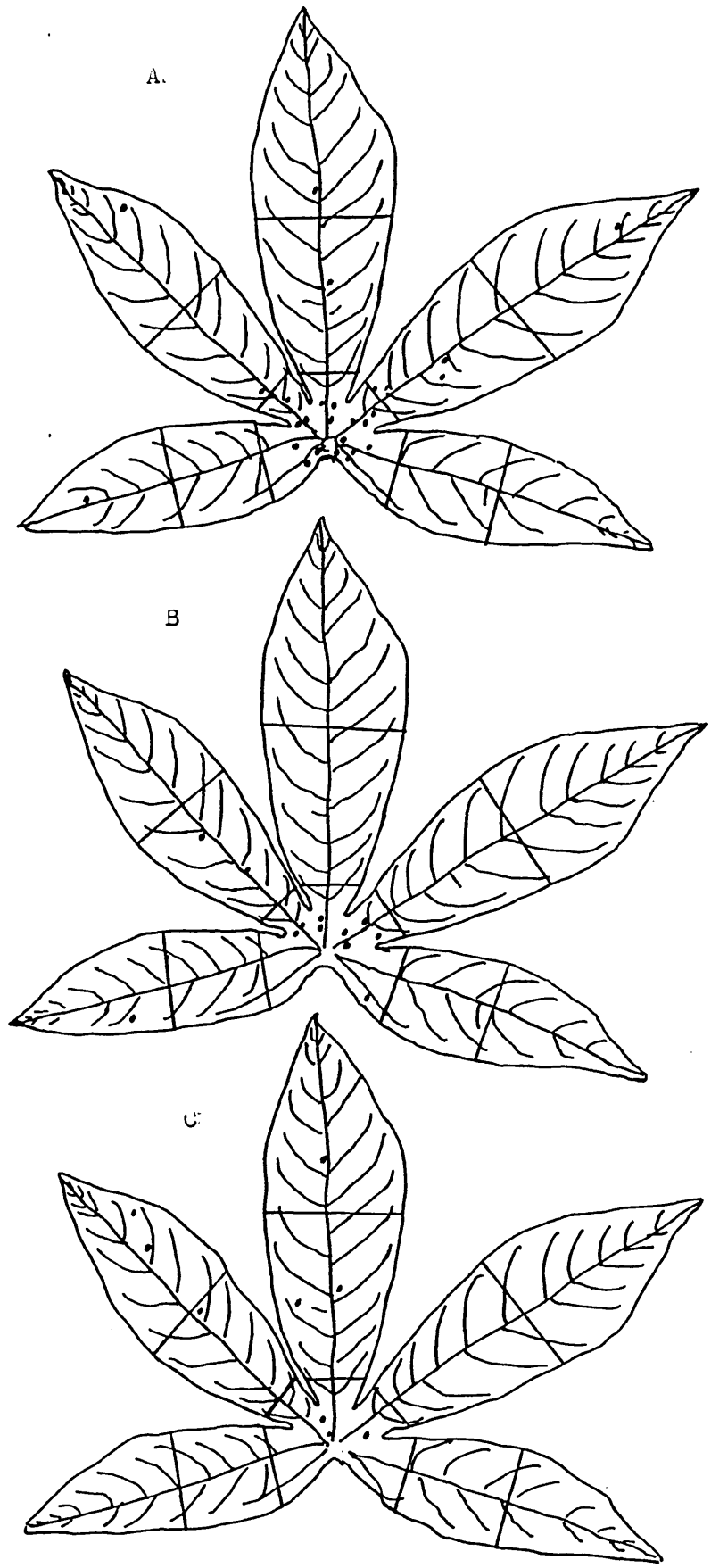


Fig. 7. Distribution of female CGM on plam, middle and distal sections on old cassava leaf at 6 ($_A$), 18 ($_B$) and 24 ($_C$) hours after introduction

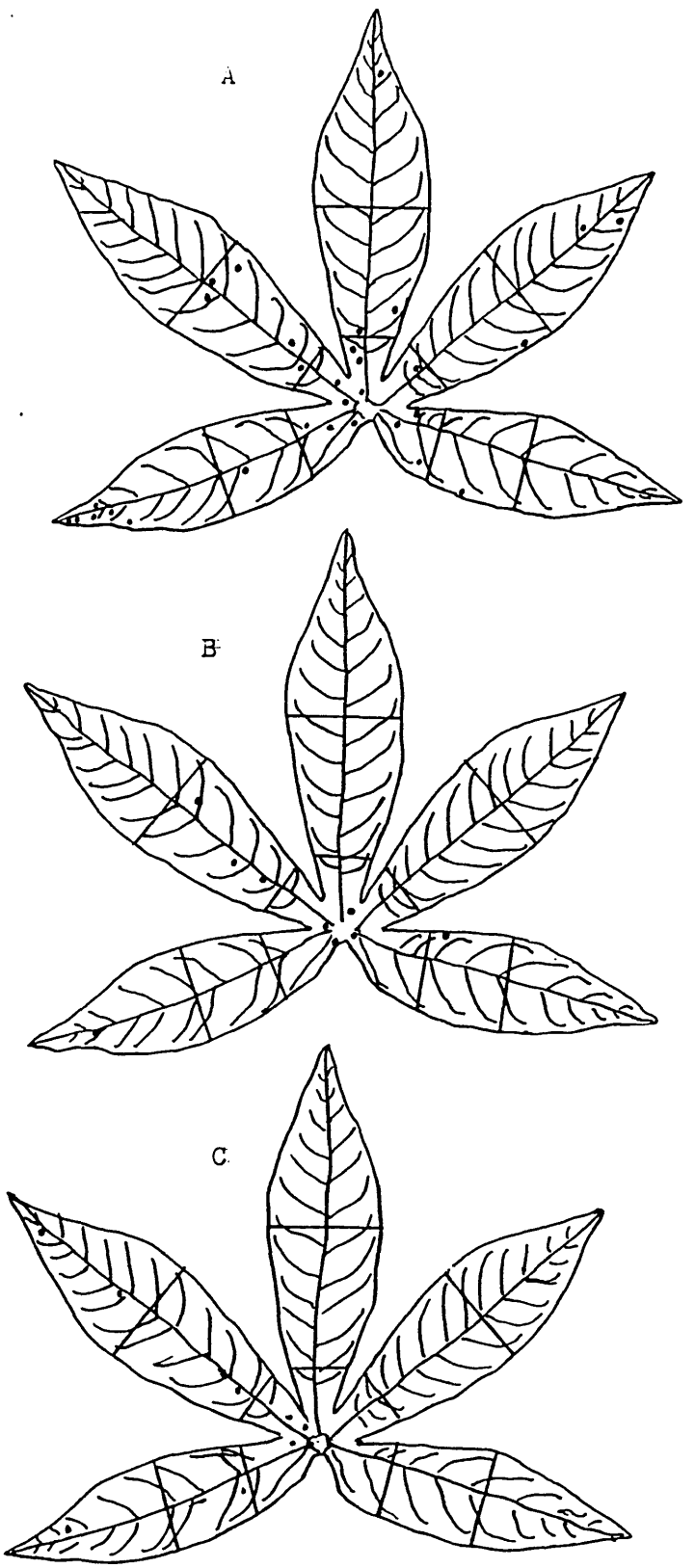


Fig. 8. Distribution of female CGM on palm, middle and distal sections of a mite damaged leaf at 6 (A), 18 (B) and 24 (C) hours after the introduction

Table 34 The comparison of the distribution of each age group on the leaf sections of young fully expanded leaves 6, 18 and 24 h after introduction

Time hours	CGM age groups	Mean density (±SE; mites/cm^2) Leaf section Palm	Middle	Distal	lsd 5%
6	Females	2.33±0.47 a	1.28±0.21 ab	0.86±0.17 b	0.35
	Males	0.41±0.10 a	0.14±0.02 b	0.11±0.06 b	0.08
	Deutonymphs	4.71±0.54 a	0.99±0.13 b	0.23±0.04 c	0.28
	Protonymph	4.45±0.98 a	1.09±0.11 b	0.42±0.11 b	0.49
	Larvae	2.29±0.61 a	0.69±0.09 b	0.48±0.06 b	0.35
18	Females	2.14±0.31 a	1.24±0.12 b	0.87±0.18 b	0.26
	Males	0.26±0.06 a	0.08±0.02 b	0.07±0.03 b	0.09
	Deutonymphs	4.76±0.85 a	0.98±0.07 b	0.20±0.04 c	0.38
	Protonymphs	4.59±0.75 a	1.13±0.13 b	0.40±0.15 b	0.40
	Larvae	2.28±0.63 a	0.74±0.11 b	0.55±0.07 b	0.38
24	Females	1.56±0.27	1.15±0.14	1.01±0.20	
	Males	0.25±0.12	0.05±0.02	0.04±0.02	
	Deutonymphs	3.04±0.67 a	0.84±0.10 b	0.17±0.05 b	0.36
	Protonymphs	4.88±0.93 a	1.14±0.15 b	0.34±0.14 b	0.48
	Larvae	2.33±0.69 a	0.73±0.11 b	0.54±0.05 b	0.39

Means within the rows followed by the same letter do not differ significantly at the 5% level
lsd values are based on square root + 0.5 transformed data

Table 35 The population of each CGM age-group on each leaf section of young fully expanded leaves throughout the experimental period

Leaf part	CGM age group	Mean density (+SE mites/cm^2) Time (hours) 6	18	24	lsd 5%
Palm	Females	2.33±0.47 a	2.14±0.31 a	1.56±0.27 b	0.13
	Males	0.41±0.10	0.26±0.06	0.25±0.12	
	Deutonymphs	4.71±0.54 a	4.76±0.85 a	3.04±0.67 b	0.28
	Protonymphs	4.45±0.98	4.59±0.75	4.88±0.93	
	Larvae	2.29±0.61	2.28±0.63	2.33±0.69	
Middle	Females	1.28±0.21	1.24±0.12	1.15±0.14	
	Males	0.14±0.02 a	0.08±0.02 ab	0.05±0.02 b	0.40
	Deutonymphs	0.99±0.13	0.98±0.07	0.84±0.10	
	Protonymphs	1.09±0.11	1.13±0.13	1.14±0.15	
	Larvae	0.69±0.09	0.74±0.11	0.73±0.11	
Distal	Females	0.86±0.17	0.87±0.18	1.01±0.22	
	Males	0.11±0.06	0.07±0.03	0.04±0.02	
	Deutonymphs	0.23±0.04	0.20±0.04	0.17±0.05	
	Protonymphs	0.42±0.11	0.40±0.15	0.34±0.14	
	Larvae	0.48±0.06	0.55±0.07	0.54±0.05	

Means within the row followed by the same letter do not differ significantly at the 5% level
lsd values are based on square root (+ 0.5) tranformed data

Table 36 Comparison of the distribution of each age group on the leaf sections of old leaves 6, 18 and 24 h after introduction

Time hours	CGM age groups	Mean density (±SE, mites/cm^2) Leaf sections Palm	Middle	Distal	lsd 5%
6	Females	1.61±0.37 a	0.23±0.02 b	0.15±0.03 b	0.28
	Males	0.55±0.17 a	0.15±0.06 b	0.06±0.04 b	0.11
	Deutonymph	2.87±0.37 a	0.51±0.11 b	0.25±0.05 b	0.39
	Protonymph	5.28±0.92 a	0.63±0.03 b	0.22±0.05 b	0.39
	Larvae	5.52±0.28 a	1.12±0.08 b	0.45±0.12 c	0.15
18	Females	1.10±0.14 a	0.14±0.03 b	0.05±0.02 b	0.13
	Males	0.42±0.11 a	0.08±0.03 b	0.02±0.01 b	0.10
	Deutonymphs	3.16±0.53 a	0.44±0.07 b	0.16±0.04 b	0.26
	Protonymphs	5.51±0.99 a	0.59±0.04 b	0.18±0.04 b	0.42
	Larvae	6.34±0.50 a	0.84±0.12 b	0.38±0.06 b	0.24
24	Females	0.96±0.16 a	0.11±0.02 b	0.06±0.02 b	0.13
	Males	0.39±0.20	0.26±0.20	0.08±0.03	
	Deutonymphs	2.62±0.42 a	0.49±0.11 b	0.17±0.04 b	0.21
	Protonymphs	5.46±0.95 a	0.58±0.05 b	0.18±0.06 b	0.40
	Larvae	6.54±0.50 a	0.94±0.13 b	0.40±0.06 b	0.24

Means within the rows not followed by the same letter differ significantly at the 5% level
lsd values are based on square root (+ 0.5) transformed data

Table 37 The population of each age-group on each leaf section of old leaves throughout the experimental period

Leaf part	CGM age group	Mean density (±SE mites/cm^2) Time (hours) 6	18	24	lsd 5%
Palm	Females	1.61±0.37	1.10±0.02	0.96±0.16	
	Males	0.55±0.17	0.42±0.11	0.39±0.20	
	Deutonymphs	2.87±0.37	3.16±0.53	2.62±0.42	
	Protonymphs	5.28±0.92	5.51±0.99	5.46±0.95	
	Larvae	5.52±0.28	6.34±0.50	6.54±0.50	
Middle	Females	0.23±0.02 a	0.14±0.03 b	0.11±0.02 b	0.03
	Males	0.15±0.06	0.08±0.03	0.26±0.20	
	Deutonymphs	0.51±0.11	0.44±0.07	0.49±0.11	
	Protonymphs	0.63±0.03	0.59±0.04	0.58±0.05	
	Larvae	1.12±0.08	0.84±0.12	0.94±0.13	
Distal	Females	0.15±0.03 a	0.05±0.02 b	0.06±0.02 b	0.02
	Males	0.06±0.04	0.02±0.01	0.08±0.03	
	Deutonymphs	0.25±0.05	0.16±0.04	0.17±0.04	
	Protonymphs	0.22±0.05	0.18±0.04	0.18±0.06	
	Larvae	0.45±0.12	0.38±0.06	0.40±0.06	

Means within the rows followed by the same letter do not differ significantly at the 5% level
lsd values are based on square root (+ 0.5) tranformed data

Table 38 Comparison of the distribution of each age group on the leaf sections of previously mite damaged leaves 6, 18 and 24 h after introduction

Time hours	CGM age groups	Mean density (±SE; mites/cm^2) Leaf section Palm	Middle	Distal	lsd 5%
6	Females	1.72±0.11 a	0.46±0.08 b	0.36±0.10 b	0.10
	Males	0.86±0.18 a	0.39±0.08 b	0.23±0.08 b	0.16
	Deutonymphs	3.29±0.24 a	0.96±0.15 b	0.55±0.11 b	0.22
	Protonymph	4.28±0.59 a	1.02±0.07 b	0.25±0.04 c	0.27
	Larvae	2.16±0.28 a	1.03±0.14 b	0.42±0.12 c	0.23
18	Females	0.81±0.15 a	0.28±0.11 b	0.09±0.01 b	0.13
	Males	0.60±0.17 a	0.19±0.03 b	0.09±0.02 b	0.16
	Deutonymphs	2.75±0.22 a	0.94±0.12 b	0.60±0.12 b	0.20
	Protonymphs	4.01±0.59 a	0.87±0.07 b	0.21±0.03 c	0.24
	Larvae	3.04±0.40 a	0.98±0.09 b	0.42±0.11 c	0.20
24	Females	0.50±0.13 a	0.14±0.03 b	0.09±0.04 b	0.09
	Males	0.34±0.11 a	0.15±0.04 ab	0.05±0.02 b	0.11
	Deutonymphs	3.39±0.39 a	0.88±0.12 b	0.38±0.06 c	0.18
	Protonymphs	3.64±0.46 a	0.94±0.05 b	0.14±0.02 c	0.21
	Larvae	3.71±0.57 a	1.09±0.10 b	0.42±0.10 b	0.31

Means within the rows not followed by the same letter differ significantly at the 5% level
lsd values are based on square root (+ 0.5) transformed data

distal portions decreased significantly after 6 h (Table 37, $\underline{P} = 0.05$), again suggesting some emigration. On previously mite damaged leaves, the densities of both adult stages on each leaf section tended to decrease after 6 h whilst that of the larvae on the palm appeared to increase significantly at the same time. On the other hand the density of the protonymphs decreased significantly ($\underline{P} = 0.05$) on the distal portions of these leaves at 24 h (Table 39).

3.9.ii The distribution of each age-group after being released simultaneously on young fully expanded leaves

The distribution of each age-group on the leaf sections tended to follow very closely that of each group when released separately on the various leaf treatments discussed in the previous section throughout the experiment. The density of each group was highest on the palm except that of females at 6 h and that of deutonymphs at both 6 and 18 h which tended to be random on all the leaf sections (Table 40).

The distribution of the age-groups on palm, middle and distal sections of the leaf is given in Fig. 9.

However the population of each age group did not change significantly on each leaf section throughout the experiment (Table 41) indicating that there wasn't significant movement between the leaf portions during the experiment.

The overall population of the age-groups similarly was more concentrated on the palm than on the other leaf sections ($\underline{P} = 0.05$) throughout the experimental period (Table 42). The palm section of the leaf probably offers adequate protection in addition to its suitablility for feeding purpose.

Table 39 The population of each age-group on each leaf section of previously mite damaged leaves throughout the experimental period

Leaf part	CGM age group	Mean density (+SE mites/cm^2) Time (hours) 6	18	24	lsd 5%
Palm	Females	1.72±0.11 a	0.81±0.15 b	0.50±0.13 c	0.14
	Males	0.86±0.18 a	0.60±0.17 ab	0.34±0.11 b	0.17
	Deutonymphs	3.29±0.24	2.75±0.22	3.39±0.39	
	Protonymphs	4.28±0.59	4.01±0.59	3.64±0.46	
	Larvae	2.16±0.28 b	3.04±0.40 ab	3.71±0.57 a	0.33
Middle	Females	0.46±0.08 a	0.28±0.11 ab	0.14±0.03 b	0.12
	Males	0.39±0.08 a	0.19±0.03 b	0.15±0.04 b	0.09
	Deutonymphs	0.96±0.15	0.94±0.12	0.88±0.12	
	Protonymphs	1.02±0.07	0.87±0.07	0.94±0.05	
	Larvae	1.03±0.14	0.98±0.09	1.09±0.10	
Distal	Females	0.36±0.10 a	0.09±0.01 b	0.09±0.04 b	0.12
	Males	0.23±0.08 a	0.09±0.02 ab	0.05±0.02 b	0.09
	Deutonymphs	0.55±0.11	0.60±0.12	0.38±0.06	
	Protonymphs	0.25±0.04 a	0.21±0.03 a	0.14±0.02 b	0.04
	Larvae	0.42±0.12	0.42±0.11	0.42±0.10	

Means within the rows folloeed by the same letter do not differ significantly at the 5% level
lsd values are based on square root (+ 0.5) tranformed data

Table 40 Comparison of the distribution of each age group when released simultaneously on the leaf-sections of young fully expanded leaves 6, 18 and 24 h after introduction

Time hours	CGM age groups	Mean density (±SE; mites/cm^2) Leaf section Palm	Middle	Distal	lsd 5%
6	Females	0.48±0.14 a	0.14±0.04 b	0.10±0.02 b	0.14
	Males	0.43±0.16 a	0.04±0.01 b	0.02±0.02 b	0.15
	Deutonymphs	0.31±0.10	0.14±0.04	0.15±0.05	
	Protonymphs	0.61±0.16 a	0.15±0.02 b	0.09±0.03 b	0.12
	Larvae	0.58±0.09 a	0.16±0.02 b	0.11±0.07 b	0.12
18	Females	0.24±0.11	0.12±0.03	0.08±0.04	
	Males	0.34±0.09 a	0.06±0.02 b	0.03±0.01 b	0.10
	Deutonymphs	0.41±0.11	0.10±0.03	0.12±0.05	
	Protonymphs	0.39±0.07 a	0.15±0.04 b	0.13±0.04 b	0.09
	Larvae	0.75±0.29 a	0.12±0.03 b	0.09±0.09 b	0.25
24	Females	0.36±0.06 a	0.12±0.04 b	0.06±0.02.b	0.08
	Males	0.36±0.13 a	0.05±0.02 b	0.04±0.02 b	0.13
	Deutonymphs	0.32±0.08 a	0.10±0.02 b	0.07±0.03 b	0.07
	Protonymphs	0.54±0.16 a	0.15±0.04 b	0.11±0.04 b	0.15
	Larvae	0.41±0.15 a	0.07±0.02 b	0.08±0.02 b	0.14

Means within the rows followed by the same letter do not differ significantly at the 5% level
lsd values are based on square root (+ 0.5) transformed data

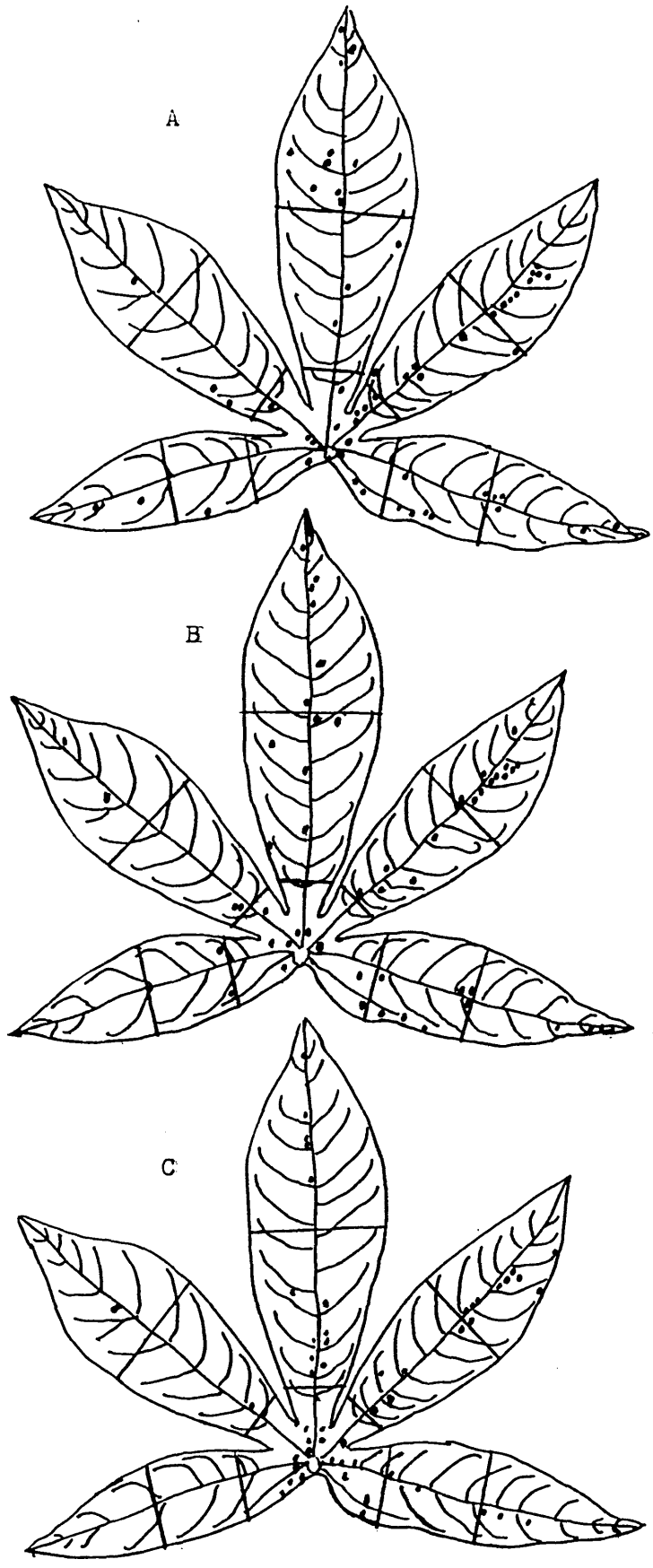


Fig. 9. Distribution of all age-groups released simultaneously on the leaf, on palm, middle and distal section of a young fully expanded leaf at 6,(A), 18 (B) and 24 (C) hours after the introduction

Table 41 Comparison of the population of each age-group when released simultaneously on the leaf sections of young fully expanded leaves 6, 18 and 24 h after introduction

Leaf part	CGM age group	Mean density (±SE mites/cm^2) Time (hours) 6	18	24
Palm	Females	0.48±0.14	0.24±0.11	0.36±0.06
	Males	0.43±0.16	0.34±0.09	0.36±0.13
	Deutonymphs	0.31±0.10	0.41±0.11	0.32±0.08
	Protonymphs	0.61±0.16	0.39±0.07	0.54±0.16
	Larvae	0.58±0.09	0.75±0.29	0.41±0.15
Middle	Females	0.14±0.04	0.12±0.03	0.12±0.04
	Males	0.04±0.01	0.06±0.02	0.05±0.02
	Deutonymphs	0.14±0.04	0.10±0.03	0.10±0.02
	Protonymphs	0.15±0.03	0.15±0.04	0.15±0.04
	Larvae	0.16±0.02	0.12±0.03	0.07±0.02
Distal	Females	0.10±0.02	0.08±0.04	0.06±0.02
	Males	0.02±0.01	0.03±0.01	0.04±0.02
	Deutonymphs	0.15±0.05	0.12±0.05	0.07±0.03
	Protonymphs	0.09±0.03	0.13±0.04	0.11±0.04
	Larvae	0.11±0.07	0.09±0.03	0.08±0.02

Means within the rows do not differ significantly at the 5% level

Table 42 Comparison of the distribution of mixed age-groups between and within leaf sections 6, 18 and 24 h after introduction

Time (hours)	Mean density (±SE, mites/cm^2) Leaf section Palm	Middle	Distal	lsd 5%
6	2.4±0.44 a	0.6±0.06 b	0.5±0.13 b	0.30
18	2.1±0.59 a	0.6±0.09 b	0.5±0.13 b	0.30
24	2.0±0.30 a	0.5±0.07 b	0.4±0.09 b	0.20

Means within the row not followed by the same letter differ significantly at the 5% level
Means within the columns do not differ significantly at the 5% level
lsd values are based on square root (+ 0.5) transformed data

3.10 Movement of an individual CGM when released singly or under crowded conditions on clean, damaged and washed leaves

3.10.1 Materials and Methods

The plants

One month old potted 'Odongbo' plants were used, with the mites being introduced onto the third leaf from the top. The leaf was traced from the undersurface as in Section 3.3.

The CGM groups

Three CGM age-groups were used: adult females, males and deutonymphs. Cohorts of each age-group were started from eggs laid in a given 24 hour period (see Section 3.3).

Experimental details

All the experiments were conducted in the laboratory at 26-27°C and 40-50% r.h.

Movement on leaves: (a) under crowded conditions:

For each test, one hundred individuals of one age-group were transferred separately from the culture to the adaxial surface of each experimental leaf using a fine camel hair brush, with 20 individuals per lobe. Ten minutes after their introduction, a single mite on the middle lobe was selected and its movement traced on the leaf for 15 mins. The leaf was held at right angles to the bench and viewed through a magni-focuser. If the mite walked onto the other side of the leaf, the observation was abandoned. There were 10 replicates for each age-group. The experiment was carried out on three successive days with one age-group per day.

(b) singly on young fully expanded leaf:

For each age-group, a single individual of each group was introduced to the adaxial surface of the middle lobe. Ten minutes after the introduction, the movement was traced as above. There were 10 replicates.

(c) singly on washed and unwashed mite damaged leaves

The experimental leaves were exposed to an initial population of 200 CGM females for a period of 72 hours. The feeding damage that resulted was quantified in mite days (see Section 3.5) as 404, 393.6 and 425.5 mean mite days respectively for females, males and deutonymphs experiments with an estimated damage score of 4 according to Yaninek's (1984) scale, with over 50% of the leaf chlorotic. Fig. 5 shows the estimated damage symptoms typically observed on the experimental leaves.

For the washed leaves, the procedure was as above, except that the experimental leaves were washed with deionized water immediately after the removal of the initial feeding females. The mean mite days for the experimental plants were 396.5, 415.2 and 405.2 respectively for females, males and deutonymphs experiments, with an estimated damage score of 4.

3.10.1.2 Experimental design

All the experiments had a completely randomized design.

3.10.1.3 Data collected

For each experiment, the proportion of time spent moving was recorded. The time spent on the lamina, midrib or edge (see Fig. 10 for the leaf parts) and the time spent on each lobe was recorded.

3.10.1.4 Analysis of data

The data were analysed using one way analysis of variance and t-test



Fig. 10. Diagrammatic representation of a cassava leaf showing the lamina (a), the midrib (b) and the edge (c) sections

depending upon the comparison. Proportion of time of activity or inactivity out of the 15 minutes of observation was transformed using arc-sine or square root with 0.5 added to each datum if there were zeros in the data.

3.10.2 Results

3.10.2.i Time of activity of each age-group

Each age-group spent a significantly greater proportion of the 15 minutes in walking than that spent standing still when the individuals were alone on the variously treated leaves ($P < 0.01$). However males on previously mite damaged leaves and deutonymphs on young fully expanded leaves, spent approximately equal periods in both movement and resting (Table 43).

In Figs. 11, 12 and 13, movement of deutonymphs, males and the adult females respectively is shown on the various leaf treatments.

The age-groups tended to respond differently in their activities when individuals of each group was observed under crowded condition. Under these conditions females spent relatively equal proportion of the 15 minutes moving and standing still; males spending most of the time walking whilst the deutonymphs rested for the greater period of the time (Table 43).

3.10.2.ii A comparison of time of activity between the age-groups within a treatment and of each age-group between the treatments

Adult females and males did not differ in the proportion of time each group spent in walking on young fully expanded leaves when the individuals were observed alone. However the activities of the deutonymphs tended to be reduced on the same leaves although they

Fig. 11. Movement of CGM deutonymph observed for 15 minutes on (A) young, (B) mite damaged (unwashed) (C) under crowded and (D) on mite damaged washed leaves

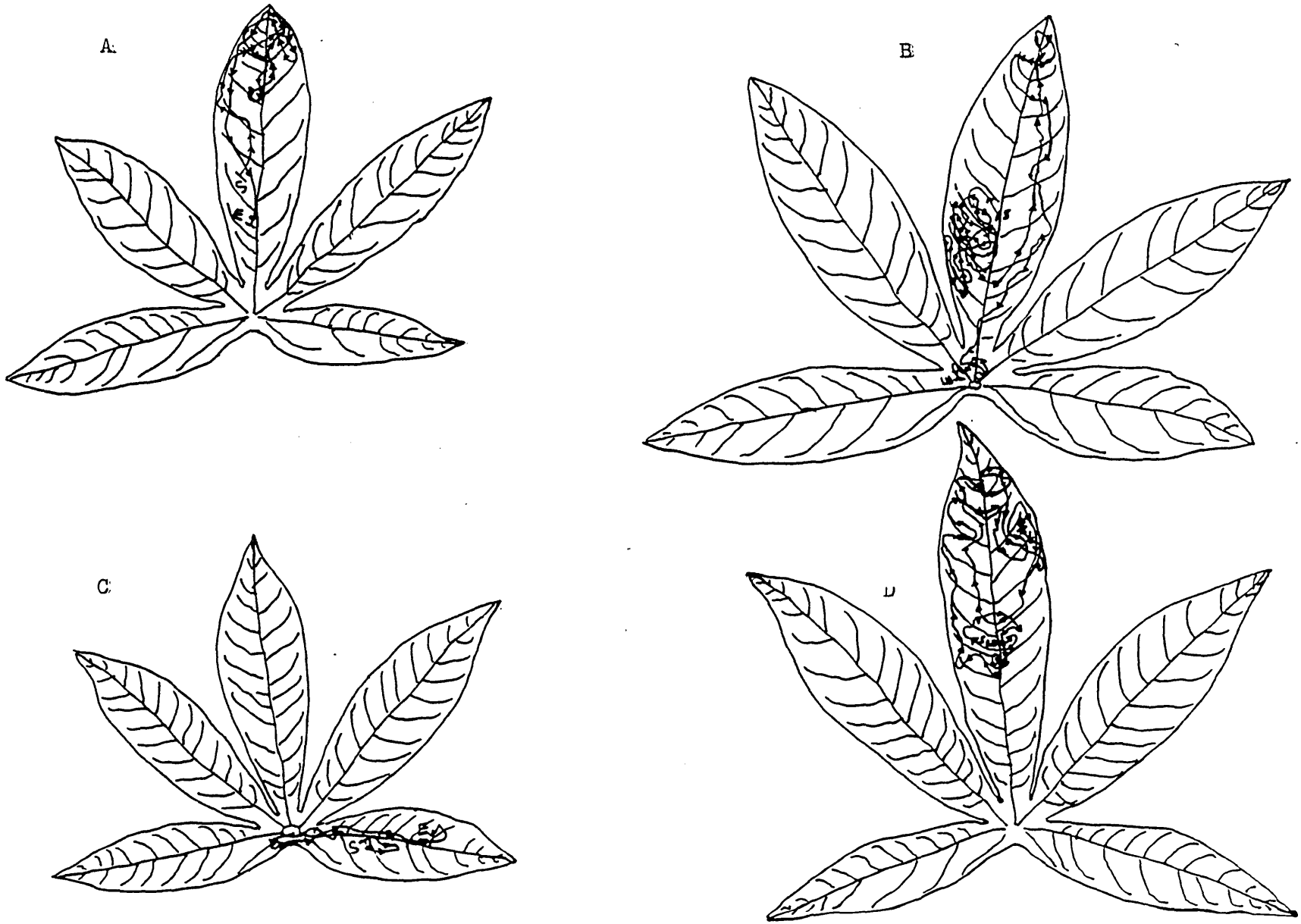


Fig. 12. Movement of adult male CGM during 15 minute period on (A) young, (B) mite damaged unwashed, (C) under crowded and (D) on mite damaged washed leaf

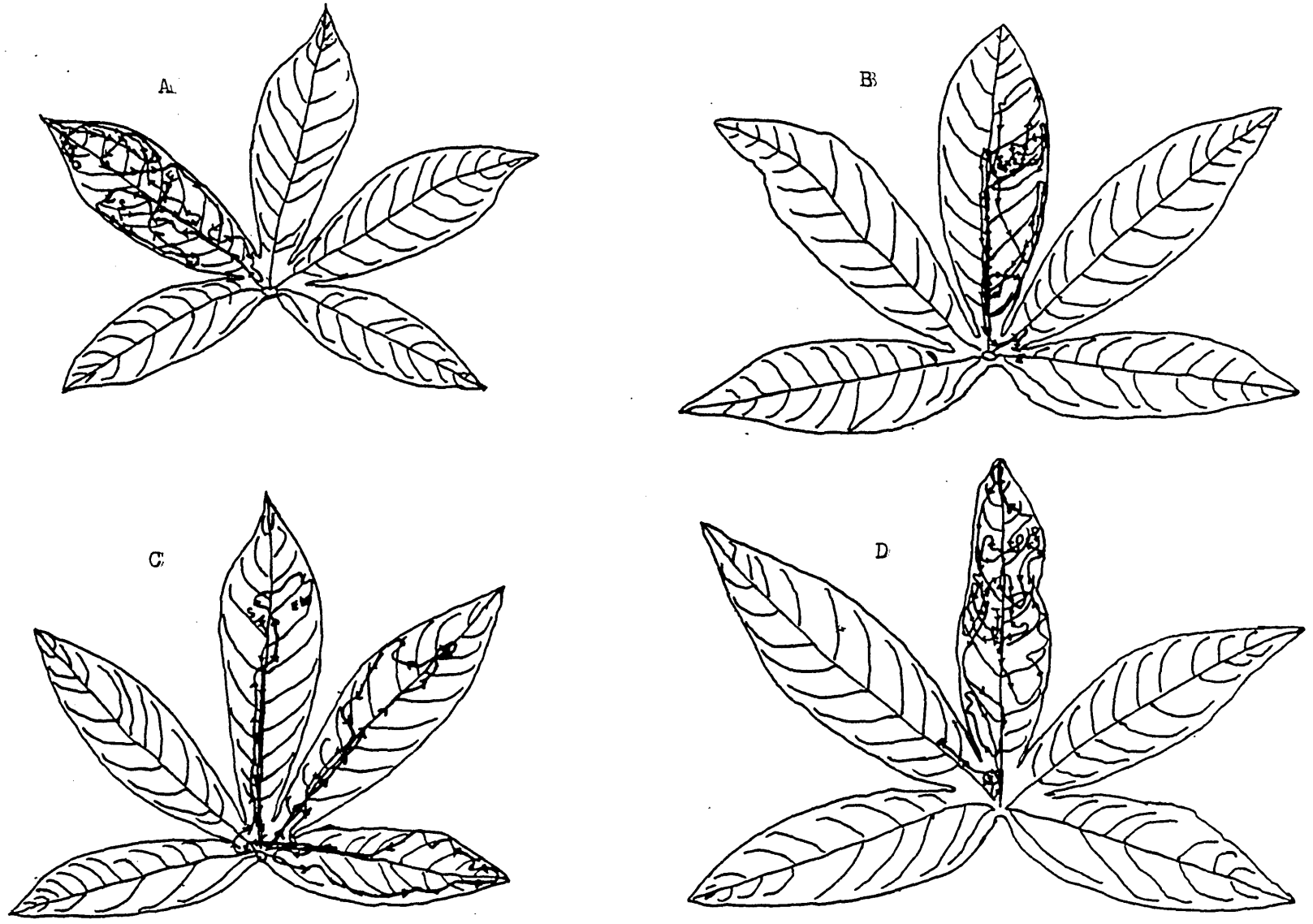


Fig. 13. Movement of adult female CGM on (A) young, (B) mite damaged, (C) under crowded and (D) mite damaged leaf, during 15 minutes of observation

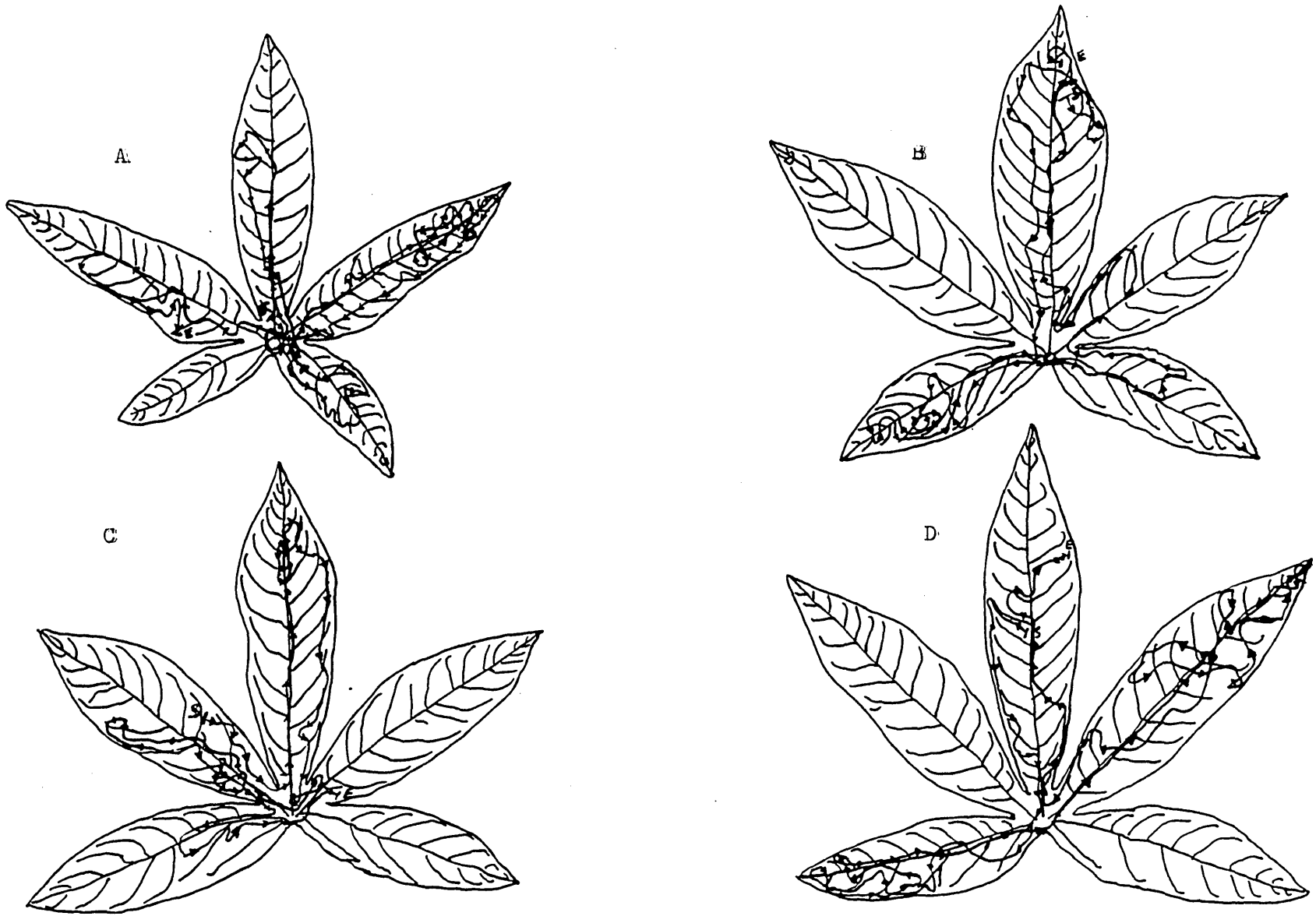


Table 43 Proportion of time spent moving during 15 minutes by each age group on the variously treated leaves

Experimental leaf	CGM age group	Proportion of time (±SE)
Young fully expanded	Females	0.65±0.04**
	Males	0.58±0.04**
	Deutonymphs	0.48±0.05NS
Previously mite damaged	Females	0.69±0.03**
	Males	0.49±0.06NS
	Deutonymphs	0.61±0.04**
Previously mite damaged washed	Females	0.69±0.02**
	Males	0.77±0.03**
	Deutonymphs	0.62±0.03**
Under crowded condition	Females	0.48±0.03NS
	Males	0.62±0.05**
	Deutonymphs	0.31±0.05**

** Time spent moving or resting significantly greater than that spent resting or moving at the 1% level (t 0.01, 18df = 2.88)
NS = not significant at 5% level (t 0.05 18df = 2.101)
Statistical analysis was performed on arc sine transformed data

differed significantly only from the females under similar conditions (Table 44). On previously mite damaged (unwashed) leaves both the adult females and the deutonymphs were more active than the males. The reduced activities of males on these leaves could be accounted for by some substances left by the initial feeding females that arrested them. When the previously mite damaged leaves were washed before the introduction of the mites, the response of the mites particularly the males changed and became more mobile than the other groups except the females ($P = 0.05$, Table 44). Under crowded conditions adult males and females both tended to be more active than the deutonymphs (Table 45) indicating that the presence of other mites of the same group had more effect on the immature than the adult groups.

The response of each age-group to the different leaf conditions indicated that their activities were influenced by the leaf conditions. Adult males were more active on the previously mite damaged and washed leaves than on the other leaves when released alone (Table 44) whilst the activities of deutonymphs were significantly reduced on young fully expanded leaves than that on the other leaves under similar conditions of the release. However adult females tended to be about equally mobile under the different conditions of the leaves, suggesting that factors other than the leaf conditions could reduce the activities of this group. The presence of other mites of the same group affected the activities of each group except that of the males (Table 45). Adult females and deutonymphs were less active under crowded conditions than when they were alone whilst adult males showed more or less similar activities under the two conditions.

Table 44 A comparison of the proportion of time of activity between the age-groups within a treatment and of each group between treatments

Activity	CGM group	Proportion of time (± SE) Experimental leaves: Young fully expanded		Mite damaged		Mite damaged washed		lsd 5%
Moving	Females	0.65±0.04	A	0.69±0.03	A	0.69±0.02	AB	
	Males	0.58±0.04	ABb	0.49±0.06	Bb	0.77±0.03	Aa	0.52
	Deutonymphs	0.48±0.05	Bb	0.61±0.04	Aa	0.62±0.03	Ba	0.46
	lsd 5%	0.49		0.51		0.29		

Means within a column followed by the same capital letter do not differ significantly at the 5% level
Means within a row not followed by the same lower case letter differ significantly at the 5% level
lsd values are based on arc-sine transformed data

Table 45 A comparison of the proportion of time of activity between age-groups and of each age group between crowded and solitary conditions

Activity	CGM age group	Proportion of time (± SE) Treatment: Crowded		Solitary		t-value
Moving	Female	0.48±0.03	A	0.65±0.04		3.48**
	Males	0.62±0.05	A	0.58±0.04		0.48NS
	Deutonymphs	0.31±0.05	B	0.48±0.05		2.45*

Means within the column under crowded conditions followed by the same capital letter do not differ significantly at the 5% level
*, ** Significant at 5% and 1% level respectively (t. 0.05, 18df and t. 0.01, 18df = 2.101 and 2.88 respectively)
t and lsd values are based on arc-sine transformed data

3.10.2.iii Time that each age-group spent on the leaf parts of the different leaf treatments

As a generalization for all leaf types, the greater proportion of the 15 minutes was spent on the lamina by all the age-groups, with the least time spent on the edge of the leaf (Table 46). However, under crowded conditions the individuals of all the age-groups spent relatively similar periods on the midrib and on the lamina. Similar results were observed for the deutonymphs on young fully expanded leaves and for the adult males on damaged unwashed leaves. The greater proportion of the time spent on the lamina than that on the other parts could be attributed to the activities of the mites which concentrated on this part of the leaf. Resting on the other hand might have accounted for the similarly greater proportion of the 15 minutes spent on the midrib observed on some of the leaves.

The proportion of time each age-group spent on each leaf portion tended to differ between the age groups however these differences were not found on all the portions except on damaged unwashed leaves (Table 46).

3.10.2.iv Rate of movement of each age-group on the different leaf treatments

The speed of movement of each age-group did not differ between the different leaf treatments when the individuals were introduced alone (Table 47).

However the speed of the adult females and the deutonymphs was significantly reduced under crowded compared with that when alone. Males on the other hand moved more or less at the same speed under both the crowded and solitary conditions (Table 48).

Table 46 Proportion of time spent on lamina, midrib and edge of the leaf by each age-group on various experimental leaves

Experimental leaf	CGM age group	Proportion of time (± SE) Leaf part Lamina	Midrib	Edge	lsd 5%
Crowded condition	Females	0.45±0.03abA	0.51±0.04A	0.04±0.01bB	0.04
	Males	0.36±0.07bA	0.53±0.08A	0.11±0.03aB	0.10
	Deutonymph	0.55±0.08aA	0.43±0.08A	0.02±0.01bB	0.10
	lsd 5%			0.03	
Young fully expanded	Females	0.61±0.01A	0.37±0.04B	0.02±0.01bC	0.04
	Males	0.63±0.06A	0.34±0.06B	0.03±0.01bC	0.07
	Deutonymph	0.50±0.04A	0.42±0.04A	0.08±0.01aB	0.06
	lsd 5%			0.18	
Mite damaged unwashed	Females	0.73±0.04aA	0.21±0.03bB	0.06±0.01bC	0.04
	Males	0.37±0.05bA	0.49±0.08aA	0.14±0.04aB	0.09
	Deutonymphs	0.60±0.04aA	0.36±0.04abB	0.04±0.01bC	0.05
	lsd 5%	0.06	0.08	0.04	
Mite damaged washed	Females	0.66±0.05A	0.32±0.05B	0.02±0.00bC	0.06
	Male	0.73±0.03A	0.24±0.03B	0.03±0.01abC	0.04
	Deutonymphs	0.61±0.03A	0.35±0.04B	0.04±0.01aC	0.04
	lsd 5%			0.01	

Means within a column on each experimental leaf followed by the same lower case letter(s) do not differ significantly at the 5% level
Means within a row on each experimental leaf not followed by the same capital letter differ at the 5% level
lsd values are based on arc sine transformation

Table 47 Rate of movement of each CGM group on the experimental leaves

CGM group	Mean speed (± SE) (cm/min) Experimental leaves: Young fully expanded	Previously mite damaged	Previously mite damaged washed
Females	4.24±0.41	4.21±0.55	3.38±0.39
Males	3.93±0.51	3.15±0.27	4.16±0.32
Deutonymphs	3.21±0.29	2.50±0.30	3.12±0.15

Means within a row do not differ at the 5% level

Table 48 Rate of movement of each CGM group compared under crowded condition and when alone on young fully expanded leaves

CGM group	Mean speed (± SE) (cm/min) Experimental condition: Crowded condition	When alone	T value
Females	2.68±0.19	4.14±0.41	3.21**
Males	3.65±0.39	3.93±0.54	0.33NS
Deutonymphs	1.63±0.20	3.21±0.29	4.90**

** Significant at $P < 0.01$. T 0.01 18df = 2.878
t-values are based on squared root transformed data
NS = Not significant at the 5% level
t 0.05, 18df = 2.101

Both the washed and the unwashed mite damaged leaves did not appear to affect the speed of both adult females and the deutonymphs (Table 49) whilst that of the males differed significantly between the two leaf treatments (P 0.05). On the washed leaves the males moved faster than on the unwashed leaves suggesting that there was more interruption in the movement of individuals on the unwashed leaves which could be attributed to the presence of some arrestants.

The speed of movement of each age-group differed between the groups on all the leaves except on young fully expanded leaves. Under crowded conditions males were the fastest and the deutonymphs the slowest (Table 50). Adult males and females, each was faster than the deutonymphs on washed and unwashed mite damaged leaves respectively indicating that the adult groups were generally faster than the deutonymphs which are under the immature group.

3.10.2.v Number of lobes/leaf visited by individuals of each age group on the different leaf treatments

The number of lobes visited by individuals of each age-group when alone did not differ between the various leaves (Table 51) during the 15 minutes. However adult females visited more lobes when alone than when under crowded conditions. The other groups visited more or less similar number of lobes under both crowded and solitary conditions. The number of lobes visited on washed and unwashed mite damaged leaves did not differ significantly for the adult females and the deutonymphs (Table 52). However more lobes were visited on washed mite damaged leaves than on the unwashed leaves by adult males. The higher number of lobes visited on the washed leaves by the males could be attributed to the higher activities of the group on these leaves than that on the unwashed leaves.

Table 49 Rate of movement of each CGM group compared between washed and unwashed mite damaged leaves

CGM group	Mean speed (± SE) Experimental leaves Unwashed	Washed	T value
Females	4.21±0.55	3.38±0.39	1.06NS
Males	3.15±0.27	4.16±0.32	2.48*
Deutonymphs	2.50±0.30	3.12±0.15	2.10NS

* Significant at P 0.05 (t 0.05, 18df = 2.101)
NS = Not significant at the 5% level
t-values are based on square root transformed data

Table 50 Comparison of the rate of movement of each group under each experimental regime

CGM mite group	Mean speed (± SE) (cm/min) Experimental leaves Young crowded condition	Alone on young fully expanded	Alone on previously mite damaged	Alone on previously damaged washed
Females	2.68±0.19 b	4.23±0.41	4.21±0.55 a	3.38±0.39 ab
Males	3.65±0.38 a	3.93±0.54	3.15±0.27 ab	4.16±0.32 a
Deutonymphs	1.63±0.20 c	3.21±0.29	2.50±0.30 b	3.12±0.15 b
lsd 5%	(0.23)	NS	(0.31)	(0.22)

Means within the columns followed by the same letter do not differ at the 5% level
lsd values are based on square root transformation

Table 51 Mean number of lobes visited by each age-group in 15 min

Age-group	Mean number of lobes (± SE) Treatments: Young fully expanded leaves	Mite damaged leaves: unwashed	Mite damaged leaves: washed
Females	1.7±0.3	1.1±0.4	1.3±0.3
Males	0.7±0.3	0.6±0.3	1.2±0.1
Deutonymphs	0.2±0.1	0.2±0.1	0.2±0.2

Means within a row do not differ significantly at the 5% level

Table 52 Mean number of lobes visited by each group under crowded condition and when alone on young fully expanded leaves and on washed and unwashed mite damaged leaves

	CGM age group	Mean number of lobe (± SE) Treatments		t values
(a)		Crowded	Singly	
	Females	0.7±0.3	1.7±0.4	2.25*
	Males	0.9±0.2	0.7±0.3	0.73NS
	Deutonymphs	0.3±0.2	0.2±0.1	NS
(b)		Unwashed	Washed	
	Females	1.1±0.4	1.3±0.3	0.46NS
	Males	0.6±0.3	1.2±0.1	2.36*
	Deutonymphs	0.2±0.1	0.2±0.2	NS

* Significant at 5% level; t 0.05, 18df = 2.101
NS = Not significant at the 5% level
Student's t-values are based on square root (+ 0.05) transformation

3.10.2.vi Residence time of each age-group on the lobes of introduction of various leaf treatments

The deutonymphs spent over 90% of the 15 minutes on the lobes of introduction on the different leaf treatments (Table 53). The few number of lobes visited by the deutonymphs suggests that most of the time was spent on the lobe of initial introduction.

Both the males and the females tended to spend the greater proportion of the 15 minutes on the lobes of introduction except on young fully expanded leaves for the females and under crowded conditions for the males, when individuals of each group spent approximately equal proportion of time on the lobes of introduction and on the other lobes.

Table 53 Time of residence of each age group on lobe of introduction of the various leaf treatments

Leaf treatment	CGM group	Mean time (± SE) (min) Lobe of introduction	T-value
Crowded condition	Females	11.88±1.2	4.96**
	Males	9.27±1.3	2.00NS
	Deutonymphs	14.97±0.03	
Singly on young fully expanded	Females	8.46±1.0	1.63NS
	Males	11.37±1.5	3.93**
	Deutonymphs	14.30±0.5	
Mite damaged unwashed	Females	12.31±0.9	6.58**
	Males	13.00±1.0	7.34**
	Deutonymphs	13.50±0.4	
Mite damaged washed	Females	10.95±1.1	4.04**
	Males	11.46±0.9	3.63**
	Deutonymphs	14.50±0.5	

** Time spent on lobe of introduction, significantly greater than that spent on other lobes, at 1% level (5 0.01, 18df = 2.88)
NS = Not significant at the 5% level (5 0.05, 18df = 2.101)
Student's 't' val ues are based on square root (+ 0.05) transformation

3.11 Discussion

3.11.1 Emigration behaviour of age-groups

The results from both the age groups released separately (Section 3.1) and those started from populations of larvae (Section 3.2) indicated that emigration occurred in nearly all the age-groups. However, differences between the age groups were found in the number of individuals of each age group that left the leaves.

Adult females had the highest percentage of emigrants whilst larvae had the least (Table 1). In Section 3.2, the number of individuals that emigrated from the adult age-groups was greater than that of the immature groups (Table 5).

The tendency for adult tetranychid females to emigrate has been reported by Hussey & Parr (1963). These authors found that the teneral and, to a lesser extent, the ovipositing females of T. urticae tended to emigrate from the leaves on which they had developed or had inhabited, even when these leaves were still suitable. Yasuda (1979) also reported similar emigration behaviour for P. citri.

Limited emigration by the immature age groups and adult males in the presence of other age groups has also been reported by Hussey & Parr (1963) and by McMurtry (1970).

However all age-groups tended to emigrate when the condition of the leaves is deteriorating or under crowded conditions when intraspecific competition increases (Hussey & Parr, 1963; Mitchell, 1973). Leaf condition and emigration behaviour of the age-groups is considered in later discussion.

When studying the emigration behaviour of Panonychus citri, Tashiro

(1966) recovered individuals of each age-group in the following order of magnitude: females, deutonymphs, protonymphs, adult males and larvae. In the present study the number of adult males which emigrated when the developing populations reached the adult stage did not differ from that of females. The enhanced emigration of males observed in this study could be due to competition for suitable mates within the colonies. The tendency for females to emigrate has nonetheless been demonstrated in the study. The effect of density as a cause of emigration, as reported by Mitchell (1973), was also demonstrated in Section 3.1. At densities 100 and 50, more females emigrated than at the lower densities. The percentage of emigrants from each of the immature age-groups did not differ between the different densities.

3.11.2 Effect of leaf condition on distribution and movement of age groups

The number of each age-group that remained on the leaves under different conditions and their distribution patterns differed between the age-groups. The main emigration of each group appeared to have occurred within the first 6 h of introduction with the highest percentage of emigrants recorded from males on each leaf treatment.

Under the good condition of the leaves (i.e. young and fully expanded) emigration by all the groups except males was limited. The males that remained were therefore more widely distributed than the other groups (Table 4). After 6 hours further significant emigration occurred with males and also with the deutonymphs when individuals of the latter group became adults (Table 4).

Adult groups were more widely distributed on old and mite damaged leaves and this could reflect the low population density after the majority had emigrated within the first 6 hours. Emigration by the adult

females and the immature groups was much less when the leaf condition was favourable. However, adult males and the teneral females demonstrated a strong tendency to emigrate, even under the same conditions.

Rapid dispersal of males when released alone on the host plant has been reported by Putman (1970) who observed that male P. ulmi released on midleaves of seedling peach trees dispersed faster and farther than adult females. The absence of suitable mates probably prompted the rapid dispersal.

Hussey and Parr (1963) reported limited dispersal of ovipositing T. urticae from bean leaves in reasonable condition. However, they reported a strong tendency for the teneral females to emigrate irrespective of leaf condition and mite density. The present study confirmed this tendency, with the females dispersing when they had become teneral adults, resulting in significant decrease in their density by 24 hours.

The low nutritional quality of senescent leaves, coupled with changes in their physical structure and deposition of unfavourable substances such as wax, has been correlated with reduced fecundity of many tetranychid species (Van de Vrie et al., 1972). Both field and laboratory observations indicated that T. urticae dispersed en masse away from senescent foliage (Suski & Naegele, 1963; Boykin & Campbell, 1984; Margolies & Kennedy, 1985), in the present study old leaves tended to be less favourable to adults with 67% of the females and over 80% of the males leaving the leaves. The percentages of emigrants from the immature group were from deutonymphs to larvae, 48.2, 29.6 and 4.0 respectively indicating a much reduced tendency to emigrate, even under less favourable conditions.

The distribution pattern of each group and their density tended to remain constant except for the females indicating that emigration after 6

hours was minimal (Table 8). The response of each age-group to the mite damaged leaves was very similar to that on old leaves. Nearly 57% of females and 69% of the males left the leaves within the first 6 h. As with old leaves, the reduced nutritional quality of the damaged leaves probably prompted the dispersal of the ovipositing females, which require more food for their role in reproduction. Males on the other hand emigrated in search for suitable developing females to mate. Dispersal of adult tetranychid females from mite damaged leaves was reported by Fleschner et al. (1956); Hussey and Parr (1963); Suski and Naegale (1966); Bernstein (1984); Boykin and Campbell (1984) and Margolies and Kennedy (1985).

Despite the poor condition of the leaves, a significantly lower percentage of each immature group left the leaves than the adult groups. The difference in emigration observed between the ovipositing females and the immature groups may be due to differences in the food requirements of the two groups. Harrison and Karban (1980) reported that adult female T. urticae emigrated in search of undamaged leaves whilst immature stages responded to a lesser extent. Within the first 6 h only about 30% of the deutonymphs, 31.8% of the protonymphs and 9.8% of the larvae had left the experimental leaves. Such low emigration by these age groups is in agreement with the suggestion that immature group of tetranychid mites tend to remain on leaves on which they had developed (Karban & English-loeb, 1988).

The distribution pattern and density of most age-groups remained fairly constant throughout the experiment on each experimental leaf indicating that further significant emigration after 6 h was limited. Neither the population nor the distribution pattern of each age-group on each lobe showed evidence to suggest that the groups preferred particular lobes on the leaf. However differences between lobes in the mean

distance between individuals and their mean number per lobe for some groups (Tables 6, 7, 9, 10, 12 and 13) suggested that individuals of these groups remained more abundantly on some lobes after the main dispersal (within the first 6 h) than on others.

3.11.3 Effect of CGM slurry on the behaviour of CGM age-groups

The presence of CGM slurry on the proximal portion of the leaves affected the distribution of almost all the age-groups. However, the extent of the response differed between the groups. The presence of slurry resulted in most groups becoming more widely distributed, reflecting low population on the treated portions. Neither males nor larvae differed between the slurry treated and the untreated portions in their distribution suggesting that they were less affected than the other age-groups by the slurry.

The presence of the slurry on the leaf might affect the groups in two ways. Firstly, volatile dispersive semiochemical substances might be present which could prompt emigration. Secondly, the presence of slurry could affect the leaf texture, acting as a barrier to the mites' normal feeding. Dicke (1986) found that odours blown from mite-infested bean leaves prompted adult Tetranychus urticae to leave the odour patch, and this behaviour was attributed to the presence of a volatile pheromone on the infested leaves. It is also possible that volatile substances from the slurry affected most of the groups enhancing their emigration. Alternatively the slurry might have interfered with the normal feeding of the mites from the physical point of view; a phenomenon comparable to the leaf conditioning of Van de Vrie et al. (1972) or that discussed by Karban and English-loeb (1988).

Deionized water did not appear to affect the behaviour of most age-groups which were more closely distributed on the water treated proximal

portions than on the untreated distal portions. Higher populations of all groups were still found on the water treated portions than that on the untreated portions, except for the males and larvae which did not differ between the two. Comparison of slurry and of deionized water on the behaviour of each age group indicated that water did not deter the mites in the same way as the slurry, because the water treated proximal portion supported higher populations of all the age-groups except males which had a more or less similar populations on the corresponding proximal portions of the two treatments (Table 23).

The population of females on the slurry free distal portions was significantly lower than that on the corresponding portions of the control treatment. The nymphal populations, on the other hand, were higher on the slurry free distal portions than that on the corresponding portions of the water treated leaves.

The age-group distribution on the proximally slurry treated leaves suggested that the majority of individuals avoided the slurry residue either by migrating to the slurry-free portions or by leaving the leaves altogether. More females therefore might have emigrated from the leaves altogether, whilst the two nymphal stages tended to migrate to the distal slurry free portions. The males and larvae did not differ on the distal portions of both the slurry treated and the control leaves.

When the leaves were treated with slurry on the distal portion, most individuals of all the age-groups settled on the proximal slurry free portion (Table 19). However, the strong tendency for males to migrate was again demonstrated in this experiment, with a high percentage of males leaving the treated leaves within the first 6 h after introduction. More mites of all ages appear to have emigrated from the slurry-treated leaves than from the water treated leaves. The immature age-groups had

the lowest percentage of emigrants, particularly from the water treated leaves, indicating that this treatment did not deter their settling on the treated parts.

3.11.4 Effect of introduction of all age-groups simultaneously on the behaviour of each individual group and on the total population

The mean distance between individuals comprising all the active age groups introduced simultaneously remained fairly constant throughout the experimental period. The density and number per lobe similarly did not differ, suggesting that emigration after 6 h was insignificant.

The distribution pattern and the population on individual lobes remained fairly constant througout the experiment. Howevèr the overall mean distance between individuals and the overall mean number tended to differ between the lobes, suggesting either some movement between lobes or non-random distribution of the individuals earlier following their introduction to the leaves.

For the individual age-groups the distribution pattern and density of each group remained fairly constant throughout the experiment. However both parameters differed between groups, but only at 6 h, with females being more widely distributed than the other groups (with the exception of the males which were excluded in the analysis of the distance between individuals). Males had the lowest density of all the group reflecting their dispersive behaviour. The distribution and population of each group on individual lobes remained fairly similar throughout the experiment. The differences between lobes in the overall mean distance between individuals and in the overall mean number observed for some of the groups were probably due to the reasons given above for the total population.

Evidence from the distribution pattern and density of both the individual age-groups and of the total population showed that the main dispersal occurred within the first 6 hours of the introduction. A mean percentage of 28.6±4.8 of the mite population left the leaf whilst that of the individual age-groups were females 25.0±7.42; males 65.0±8.37; duetonymphs 20.0±5.70; protonymphs 17.0±4.64 and larvae 16.0±6.78. The higher emigration by males in the presence of the other age groups is rather unusual. Putman (1970) reported rapid dispersal of Panonychus ulmi males when released alone on a leaf. However, he indicated that this emigration was reduced when other groups were present. The adult females were probably not attractive to the males as they were already ovipositing, whilst the deutonymphs were too young to arrest the males within the first 6 h. Apart from the rapid dispersal of the males, the emigration behaviour of the other groups are similar to that reported by Hussey and Parr (1963) on other tetranychid mites. These workers noted that ovipositing females did not disperse much, unless under population pressure or food deterioration. Similarly the immature groups tended to remain on the leaves on which they had developed, dispersing only under worsened condition of the host plant (Perring et al., 1987). The emigration observed within the first 6 h for the ovipositing females and the immature groups might be attributed to changes in the environment due to their transfer to new leaves.

3.11.5 Leaf age and leaf condition: their effect on the behaviour of each age-group

Both leaf age and leaf condition affected the behaviour of the age-groups. Significantly more adult females settled on young fully expanded leaves than on the other leaf treatments (Table 32). The number of females which remained on leaves treated with CGM slurry on the distal portions was also greater than that of the other leaf treatments, apart

from the young fully expanded leaves.

The preference for the young fully expanded leaves by the adult females suggests that these leaves are nutritionally superior to the old leaves and also to the mite damaged leaves.

The presence of CGM-slurry tended to discourage females from settling. However its presence on the proximal portion tended to discourage more individuals from settling than when present on the distal portion. This response suggests that the proximal portions of the leaves are more favourable than the distal portions even when these portions are free of the slurry.

A number of authors have indicated that leaf age and leaf condition are important factors determining their colonization by many tetranychid species. Leaf ageing and other factors leading to leaf deterioration therefore would tend to prompt emigration rather than encouraging their settlement. Thus McMurtry (1970) reported decreasing populations of female Oligonychus punicae with increasing damage to avocado leaves, while Bernstein (1984) noted that emigration of T. urticae was prompted by damage to the plants by the mites. Emigration due to leaf deterioration as a result of mite feeding has also been reported by Perring et al. (1987) for the two spotted mite on Cantaloupe Cucumis melo L. var. reticulatus; by Wilson et al. (1983) for the same mite on cotton, while Hussey and Parr (1963) observed similar trends for the same species on Vicia faba. Ageing leaves tend to have similar effect on the behaviour of adult tetranychid females as damaged leaves due to mite feeding (Karban & English-loeb, 1988). Thus Yaninek (1985) reported the emigration of adult female CGM up the plant from the ageing leaves to the younger leaves.

The presence of CGM slurry might have elicited a deterrent signal or

acted as a physical barrier which interfered with the feeding of the mites. With the adult males, significantly more individuals remained on the mite damaged unwshed leaves throughout the experimental period than that on other leaves. Clearly the mite damaged unwashed leaves might have contained some arrestant substances following the feeding of the adult females.

A number of authors have reported reduced emigration of adult males of several tetranychid species from leaves on which other age groups were present, particularly the deutonymphs at the teliochryalis stage (McMurtry, 1970; Putman, 1970; Mitchell, 1973; Perring et al., 1987).

The distribution of each immature age-group differed between leaf treatments (Table 32). The highest deutonymph populations were found on young fully expanded leaves followed by that on mite damaged leaves, indicating both an increasing food requirement for this group and also a tendency to remain on the natal leaves.

The lowest population of deutonymphs were found on both old and on distally slurry-treated leaves. The distribution of the protonymphs followed closely that of the deutonymphs except that the next highest population was on leaves treated with slurry on the distal half. The lowest populations of protonymphs were found on both the mite damaged leaves and on leaves treated with slurry proximally. This group also appeared to tolerate the population pressure on the slurry free proximal half caused by emigration to avoid the slurry on the distal portion.

Larvae on the other hand showed a slightly different response. More were found on the old leaves, followed closely by the young fully expanded leaves and then mite damaged leaves. The proximally slurry-treated leaves tended to have the lowest population of this group, suggesting that more individuals had emigrated.

Only limited emigration of immature groups of many tetranychid mites has been reported (McMurtry, 1970; Mitchell, 1973; Perring et al., 1987; Karban & English-loeb, 1988). However these groups do emigrate under high population pressures and when conditions on the natal leaf deteriorate (Hussey & Parr, 1963).

3.11.6 The distribution of each CGM age-group on palm, middle and distal portions of the different leaf treatments

All age-groups showed a similar distribution pattern on the leaf portions of the variously treated leaves. The populations of each group were more concentrated on the palm section of all leaves although in very few cases some groups tended to distribute randomly on the leaf portions, such as females and males on young fully expanded leaves and males on old leaves (Tables 33 and 35). The concentration of individuals of each group on the palm section of the leaves could be attributed to a number of reasons. Suitability for oviposition could be one of the causes of higher concentration of individuals on the palm. Oloo et al. (1987) observed that most of the CGM eggs laid were deposited alongside or at the base of veins or midribs rather than on the open leaf surface. The palm portion, which comprises the leaf junction to the petiole, has prominent veins and midribs of the various leaf lobes, thus attracting more individuals for oviposition. However because of the smaller size of this portion relative to that of the other sections, coupled with the mite density, some individuals obviously had to settle on other portions of the leaves, probably along the midribs which are more prominent than the branching veins.

The palm portion could also be the most suitable for feeding purposes as indicated by Oloo et al. (1987) who noted that feeding activity by adult females took place at the base of the veins, or farther

away on the open leaf surface. For the immature age-groups the preference for the palm section could be explained by the presence of prominent veins and midribs which provide suitable sites for the quiescent stages. Oloo et al. (1987) observed that between 84.2-98% of the quiescent stages and exuvies were alongside veins and midrib, irrespective of the nature of the leaf surface structure and mite density. Adult males, as observed in the other sections, tended to disperse rapidly following their introduction. Their dispersal behaviour has been associated with the search for suitable age groups for mating. Despite this dispersive behaviour, their distribution nevertheless indicated that more individuals concentrated on the palm portions of the various leaves, conforming with the distribution of their mates, the developing immature groups at the teliochryalis stage.

When all the age-groups were released together, both the densities of each separate group and that of the total population were higher on the palm than that on the other leaf sections (Tables 38 and 40).

The physical surface features of leaves can act either to the advantage or disadvantage of tetranychid mites, depending on the species (Van de Vrie et al., 1972). It has long been recognized that leaf texture, vestiture and contours serve as impediments to feeding, for substrates for attachment of webbing or for direct protection from disturbing or harmful micro-climatic effects on the leaf surface. Under unfavourable conditions, weak webbers (such as Pananychus ulmi, P. citri and Eotetranychus willametti (McGregor)) tend to settle close to the midribs and veins which provide best protection (Van de Vrie et al., 1972).

Pena and Waddil (1982) reported that T. urticae and P. citri were mainly concentrated on the middle lobes of cassava leaves near the

midveins. Adult CGM females inhabit the undersurface and oviposit along, or at the base of veins near the midrib or in leaf concavities (Bellotti & Schoonhoven, 1978a; Oloo et al., 1987). However, under high population pressures, CGM tended to deposit their eggs more randomly. The above authors did not however indicate the distribution pattern from the leaf junction to the distal end. Gupta et al. (1975), when studying the distribution of Tetranychus neocaledonicus on brinjal leaves found no significant difference in the distribution of the mites between the basal, middle and distal portions of the leaves. When Pena et al. (1984) partitioned the cassava leaf into the central area (i.e. palm in the present study), the external lobes and the middle lobes in studying the distribution of the cassava mite Mononychellus caribbeanae, they found no significant difference in the density of the mites between the leaf sections. However, they reported significantly larger population of T. urticae and P. citri localized on the central leaf area compared to that on the leaf lobes. In the present study, all age-groups demonstrated a preference for the palm area.

3.11.7 The activities of individuals of three CGM age-groups under crowded conditions and when released singly on leaves of different treatments

The activities of each age-group shown in Table 42 indicated that leaf condition influenced the activities of all groups. However the extent to which each group responded differed to some extent (Tables 43 and 44).

All the groups tended to be more active on the various leaves when alone, except deutonymphs on young fully expanded leaves and males on previously mite damaged leaves, when they spent approximately similar periods in walking and resting. In the presence of other mites of the

same group, the response of each group tended to differ between groups. When males were more active under such conditions, female's activities were reduced to approximately half whilst that of deutonymphs dropped to almost one third (Table 42).

The differences in the activity of each age-group due to leaf condition and as a response between the groups are indicated in tables 43 and 44. Females were approximately equally mobile when alone, in all treatments, but did tend to be more active than when crowded.

The washing of mite damaged leaves affected the males, which became more active than on either unwashed or young fully expanded leaves. Adult males showed approximately similar activities when the individuals were alone and when they were in the presence of other males. With solitary deutonymphs, the activity on young fully expanded leaves was significantly reduced compared with that on mite damaged, washed and unwashed leaves. However in the presence of other deutonymphs, their activity became significantly reduced.

With the exception of the mite damaged unwashed leaves, the adult groups generally tended to be more active than the deutonymphs on the various leaves both under solitary and crowded conditions. Mobility by tetranychid mite is a common phenomenon depending on the age-group and conditions of the host. Mobile behaviour is associated with the dispersing group, usually the teneral females and, to a lesser extent, the reproductive females under unfavourable conditions of the leaves (Hussey & Parr, 1963).

Within-leaf movement could occur either in search of suitable sites for settlement or in the search for existing mite colonies (Sabelis, 1985b). During such movement, probing occurs to test the suitability of the host. Once the host is accepted and a preferred site is found,

settlement occurs.

The mobile behaviour of males when released alone on the plant was reported by Putman (1970). However such mobility would be reduced in the presence of the other age-groups. The initial feeding by females before the introduction of the males appeared to reduce the mobility of males. Deutonymphs, as well as the other immature groups of the tetranychid mites are known to be less mobile (Mitchell, 1973) and are generally confined to the leaves on which they develop.

The movement by deutonymphs released singly in the present study was probably due to the environmental factors. However under crowded conditions, which are more or less comparable to a colony in which they usually develop, their activity was significantly reduced. The results in Table 45 indicate that each age-group spent a significantly greater proportion of the 15 minutes on the lamina than on the other parts of the leaf. Such results might reflect the activity of the mites which has been known to take place in this particular area (Oloo et al., 1987).

Areas along the midrib have also been reported by a number of authors as favourable sites particularly for settlement by the adult females and the immature groups (Van de Vrie et al., 1972; Bellotti & Schoonhoven, 1978a; Pena & Waddil, 1982; Pena et al., 1984).

The speed of each age-group did not differ between the variously treated leaves when individuals were released singly (Table 46). However, under crowded conditions the speed of adult females and deutonymphs was significantly reduced compared with individuals of each group when alone (Table 47). On the other hand, the speed of adult males was approximately similar when alone and when crowded. However, their speed was significantly reduced when they were on mite damaged, unwashed leaves compared with that on the washed leaves. Under both the unwashed

and washed conditions of the mite damaged leaves, the speed of neither adult females nor deutonymphs differed (Table 48). The speed of each age-group on the variously treated leaves indicates that the deutonymph were generally the slowest, further evidence for their reduced role in dispersal (Table 49).

When released singly, the number of lobes visited by individuals of each group in the 15 min period did not appear to differ between the various leaves (Table 50). However, when the number of lobes visited under crowded conditions is compared with that visited under solitary conditions, it was found that more lobes were visited by females under the latter conditions. Adult males, on the other hand, visited more lobes when the leaves were mite damaged and washed than when they were unwashed, reflecting partly their activities under these conditions of the leaves.

Almost all the age-groups spent the greatest time on the lobe of initial introduction, except males under crowded conditions and females on young fully expanded leaves, which spent approximately similar periods between the lobe of introduction and on other lobes.

3.12 Conclusion

The study on the emigration behaviour of the CGM age-groups indicated that more adult males and females emigrated than the immature groups. The main dispersal for all age-groups occurred within the first 6 h of the introduction.

Under good leaf conditions, emigration by all groups except males was reduced, whilst on old and previously mite damaged leaves the groups tended to respond differently with more adults emigrating than the immature groups.

CGM-slurry enhanced emigration, probably due to the presence of dispersive semiochemicals or through contamination of the leaf. However the extent of the emigration tended to be dependent upon the leaf portion on which the slurry was present. Further investigation is required to confirm whether or not dispersive semiochemicals were involved.

Treating the leaves with deionized water did not appear to affect the behaviour of most age-groups. The presence of all the age-groups together tended to reduce emigration and resulted in a consistent distribution pattern throughout the experimental period. Although the distribution pattern and the population on the individual lobes remained fairly constant throughout the experiment, the overall mean distance between individuals and the overall mean number differed between the lobes suggesting that the initial distribution of the mites on the lobes was non-random.

The majority of mites of each group concentrated on the palm portions rather than the middle and distal portions of the leaves. This distribution could be explained by the preference for sites close to veins and midrib which can offer protection to the mites. Leaf condition

and the presence or absence of other mites of the same age-group appeared to influence the activities of each group. The differences observed in the activities of the mites under similar conditions could be explained by difference in behaviour of the age groups.

With few exceptions, it can be concluded that all the groups tended to be more active when alone on the various leaves, whilst under crowded condition the activities of deutonymphs were significantly reduced. The adults generally tended to be more active than the deutonymphs on most leaves.

More time was spent on the leaf lamina of the various leaves by all the age-groups than on either the midrib (except for young fully expanded leaves) or the edge. Leaf condition did not appear to affect the speed of movement of any group when individuals were observed under solitary conditions. However the speed of adult females and deutonymphs was significantly reduced under crowded condition.

The washing of the mite damaged leaves resulted in significantly greater speed by adult males compared with that on the unwashed leaves. The speed of adult females and that of the deutonymphs did not differ between the washed and the unwashed mite damaged leaves.

The number of lobes each group visited did not differ between the various leaves when individuals were alone. Under crowded conditions adult females visited significantly fewer lobes compared with that visited under solitary conditions.

On the other hand, adult males visited more lobes on the washed mite damaged leaves than that on the unwashed leaves.

Individuals of each group spent a greater proportion of the 15 minutes on the lobe of introduction than on the other lobes. The

activities of each age-group was studied on variously treated leaves of the same variety. Effect of different varieties on the activities of the age-groups would be worthwhile studying in the future.

SECTION 4. EXPERIMENT 2.

MOVEMENT AND DISTRIBUTION OF CGM FEMALES WITHIN THE CASSAVA PLANT.

SECTION 4

Movement and distribution of CGM females within the cassava plant

4.1 Introduction

Tetranychid mites display characteristic distribution on their host plants. For instance, at the leaf level, most species inhabit the lower surface e.g. Mononychellus spp. and Tetranychus spp. (Van de Vrie et al., 1972; Jeppson et al., 1975; Bellotti and Schoonhoven, 1978b; Pena and Waddil, 1982), although a few species do feed on the upper surfaces e.g. Oligonychus spp. (Van de Vrie et al., 1972).

The condition of the foliage and the general environment are among the factors which influence the distribution of the mites on their host plants. Mononychellus spp. inhabit the youngest leaves whereas Tetranychus spp. are usually found on the mature and older leaves, moving to the upper leaves when there has been leaf defoliation. Oligonychus spp. feed on the lower and intermediate node leaves (Bellotti and Schoonhoven, 1978b; Pena and Waddil, 1982). However the dynamics of CGM on the cassava plant is less well known and the present work was intended to generate information on movement and distribution of adult CGM females when released at various heights on the plant.

4.2 Materials and Methods

4.2.1 The Plant

Three month old potted plants with 27 leaves were used. The mites were introduced onto the youngest fully expanded leaf, middle leaf (no. 13) and to the bottom leaf.

4.2.2 The CGM group

A cohort of young adult females was used as in Section 3.3.

4.2.3 Experimental details

The plants were separated into the three groups corresponding to the site of mite introduction. There were 10 plants in each group. One hundred CGM females were first placed on 15 mm diameter cassava discs; these were then transferred to the adaxial surface of the experimental leaf where they were attached with using rubber paste. The experiment was conducted under both field and glasshouse conditions with temperature and relative humidity as shown in Appendices 1 & 2. The glasshouse experiment was carried out immediately after the field experiment.

4.2.4 Experimental design

Complete randomization. The plants were spaced 1.5 metres apart.

4.2.5 Data collection

The population per leaf was recorded three days after the introduction.

4.2.6 Analysis of data

The distribution of the mites was compared between the lower half and upper half of the plant for each site of introduction using student's t-test. Analysis of variance was used to compare the percentage of mites which remained from the plants for the different treatments.

4.3 Results

4.3.1 Field conditions

Figures 4A, B and C show the distribution of CGM 3 days after the

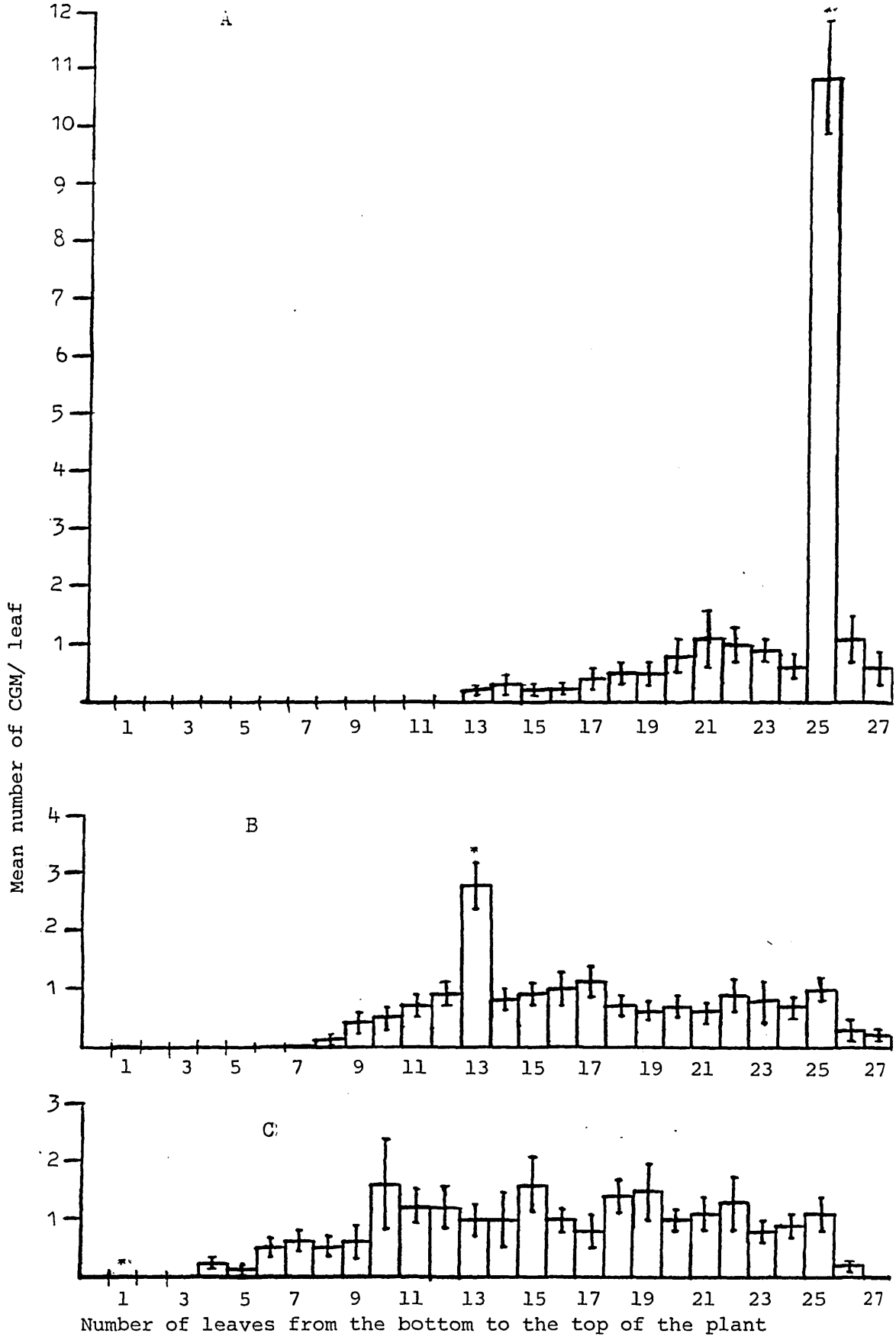


Fig. 14. Distribution of female CGM on cassava plants three days after introduction when the initial introductions were made on (A) top (B) middle and (C) bottom-most leaf under field conditions

* Initial site of CGM introduction

introduction. Movement of the mites from the youngest leaves down the plant was much reduced, as was all downward movement from the middle leaf. However, substantial upward movement took place from the bottom and the middle leaves within three days after release. Even with the release on the bottom-most leaf, the density of the CGM was significantly greater on the upper half of the plant than that on the lower part. An overall percentage of 18.73±1.6 mites remained per plant for all treatments. Significantly more CGM remained on plants where the releases were made on the bottom leaves than when released on the middle leaves ($P = 0.05$) (Table 54).

Table 55 shows the percentage of leaves on the lower and upper halves of the plants infested with the CGM three days after introduction from the three release sites. More CGM moved up the plant from both the bottom and the middle leaves than moved down from either the top or middle leaves, showing that the mites had a stronger tendency to move up than down the plant.

4.3.2 Glasshouse conditions

The distribution of the mites from the three sites was similar to that described above under field conditions, and is shown in Figures 15A, B and C. However, more mites remained on the plants under glasshouse conditions than under field conditions (Table 54). The lower population remaining under the field conditions suggest that environmental factors outside prompted greater dispersal than those in the glasshouse.

Tables 55 and 56 show the proportion of infested leaves and the population of CGM from the three sites. Significantly more individuals moved up than down the plants as found previously.

Table 54 Percentage CGM remaining on the plants three days after the introduction under both field and glasshouse conditions

Leaf of initial CGM introduction	% present
a) Under field conditions	
Top	19.3±1.0 ab
Middle	15.7±1.0 b
Bottom	21.2±2.0 a
lsd 5%	0.27
a) Under glasshouse conditions	
Top	61.6±4.2 a
Middle	47.3±3.7 b
Bottom	45.5±3.8 b
lsd 5%	0.46

Means within the column in each section followed by the same letter do not differ significantly at the 5% level
lsd values are based on arc-sine transformation

Table 55 Comparison of % leaves infested and % CGM recovered on each half of the plants when the mites were released from different initial sites under field conditions

Leaf of initial CGM introduction	% Lower half of plant	Upper half of plant	t-value
Top			
% leaves infested	1.6±1.1	52.3±3.48	15.73**
% CGM recovered	1.0±0.67	97.4±0.90	36.11**
Middle			
% leaves infested	19.4±1.2	55.8±2.77	12.17**
% CGM recovered	16.9±1.29	65.5±2.94	15.03**
Bottom			
% leaves infested	35.2±4.94	62.5±3.34	4.42**
% CGM recovered	33.5±4.69	59.9±4.16	2.58**

** Significant at 1% level, t 0.01 18df = 2.88
Student's 't' values are based on arc-sine transformation

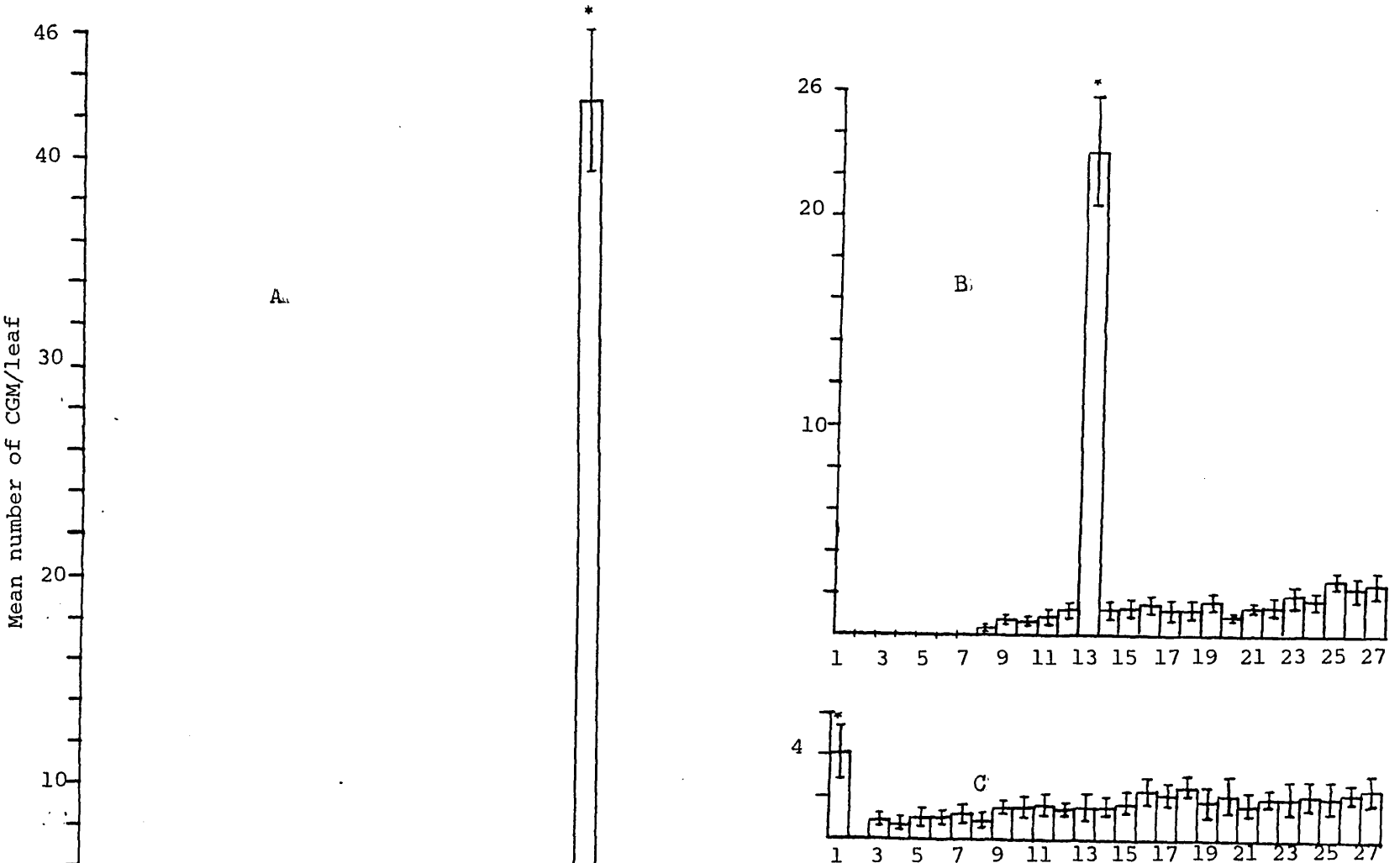


Fig. 15. Distribution of female CGM on cassava plants three days after introduction when the initial introductions were made on (A) top, (B) middle (C) bottom-most leaf under glasshouse conditions

Table 56 Comparison of % leaves infested and % CGM recovered on each half of the plants when the mites were released from different initial sites under glasshouse conditions

Leaf of initial CGM introduction	% Lower half of plant	Upper half of plant	t-value
Top			
% leaves infested	0.8±0.77	69.2±2.57	25.94**
% CGM recovered	0.2±0.27	99.3±0.3	66.23**
Middle			
% leaves infested	20.1±2.19	68.4±3.1	11.65**
% CGM recovered	7.0±1.2	44.9±2.7	13.00**
Bottom			
% leaves infested	60.9±3.73	78.6±2.75	3.84**
% CGM recovered	37.8±3.72	58.2±3.95	3.80**

** Significant at 1% level, (t 0.01, 18df = 2.88)
Student's 't' values are based on arc-sine transformation

4.4 Discussion

Differences were found in the distribution of CGM females on cassava plants when introduced to the top, middle or bottom leaves. The release of mites on the middle and bottom leaves resulted in significantly more individuals moving up than down the plant when released on top or middle leaves (Tables 55 and 56).

The results are similar to the distribution noted by other authors who have reported that CGM inhabited the upper leaves (Nyiira, 1975, 1978; Yaseen and Bennett, 1977; Byrne et al., 1983; Bellotti, 1985; Yaninek, 1985; Ezulike, 1988).

Yaseen and Bennett (1977) found that the majority of the CGM were between the upper 5th and 10th leaves. In Uganda, Nyiira (1978) reported the main population on leaves 8-10 on cassava aged between 3 and 15 months, while Ezulike (1988) observed CGM infesting the top 30 leaves, with the highest number found between leaves 3 and 12.

In the present study the tendency for CGM to move to the younger leaves, with only limited movement down the plant, was demonstrated, though it depended on the site of initial release.

Under both the field and glasshouse conditions, the highest density of mites in each treatment was on the leaf of initial release, except on the bottom-most leaves under field conditions. The density of the mites on the leaves below the top leaf of introduction appeared to decrease down the plant. In addition, when the mites were released from the bottom and middle leaves, the density appeared to increase toward the upper part of the plant. It was probable that the mites were still moving to the upper leaves when the counting was made on the third day after release (Figs.15a, b and c) and that most of the population would have finally settled on the younger leaves.

Some authors have suggested possible causes for the distribution of CGM on cassava. Braun et al. (1989) have suggested that the phenology and cassava cultivar, and the presence of predators could influence mite distribution. These authors considered that CGM could occur throughout the plant. They attributed the skewed distribution towards the upper leaves to cassava branching habit and the defoliation of the lower leaves during the dry season.

Similar preference for the upper leaves has been reported on closely related species Mononychellus caribbeanea (Mcgregor), which feeds on cassava (Pena and Waddil, 1982; Pena et al., 1984). This distribution behaviour of CGM and closely related species may be attributed to the quality of the leaves, as suggested by Nyiira (1975) and Yaninek (1985). The reduced movement down the plant from the younger towards the older leaves observed in the present study demonstrated the above phenomenon.

It is possible that factors related to dispersal could also contribute to the skewed distribution towards the upper leaves. Aerial dispersal could be more effective from the upper leaves than lower down the plant where dense canopy may constitute a barrier to such dispersal.

4.5 Conclusion

Skewed distribution toward the upper half of the plant by adult CGM females released at different sites on the plants was demonstrated. Therefore more upward movement from the lower part of the plant occurred compared with that down the plant from the top.

The higher nutritional status of the younger leaves as suggested by a number of previous authors influenced both movement and distribution of the mites on the plant. However it is speculated that the preference for the upper part of the plant to the lower half could also be attributed to

convenience for aerial dispersal.

Such position would enable the mites to spin and drift much more easily in the air than they would lower down the plant where the canopy is dense.

SECTION 5. EXPERIMENT 3.

EMIGRATION BEHAVIOUR OF THE ACTIVE STAGES OF NEOSEIULUS IDAEUS.

SECTION 5

Emigration behaviour of the active stages of *Neoseiulus idaeus*

5.1 Introduction

The possibility of using phytoseiids as predators of other mites was recognised as early as 1906 (Jeppson *et al.*, 1975). *Neoseiulus idaeus* (Denmark & Muma) is among the seven exotic phytoseiid species which have been shipped to IITA where they are being maintained for laboratory studies and for small experimental field releases (Yaninek *et al*, 1989).

The active stages of phytoseiids include the six legged larva, the protonymphs, deutonymphs and the adult stages, both females and males (McMurtry *et al.*, 1970; Sabelis, 1985). In some species such as *Amblyseius citrifolius* (Denmark and Muma) the larva feeds on young tetranychids, whilst others, such as *Phytoseiulus macropilis* (Banks), larval feeding has not been observed (Sabelis, 1985). Larvae are less motile than the other stages (Jeppson *et al.*, 1975), although Moraes and McMurtry (1981) observed that protonymphs of *Amblyseius citrifolius* were more active than both the other immature groups and the adult females. The above authors however did not give an explanation for such activity.

The emigration behaviour of phytoseiid may differ between species, and is influenced by both predator and prey densities (Eveleigh and Chant, 1982). Kuchlein (1966) reported that the migration tendency of young *Typhlodromus longipilus* (Nesbitt) females (4-9 days) did not differ significantly between densities but that it differed significantly when the females were older (16-23 days). However Kuchlein did not indicate whether or not such behaviour occurred at constant prey density.

In the absence of prey, emigration of phytoseiids tends to be rapid.

Takafuji (1977) observed that all P. persimilis females had left plants lacking prey within 4 hours of release. There is less information on the emigration behaviour of N. idaeus. The present study has been undertaken to determine the emigration behaviour of N. idaeus females and the nymphs (protonymphs and deutonymphs not discriminated). Larvae and adult males were not included in this study.

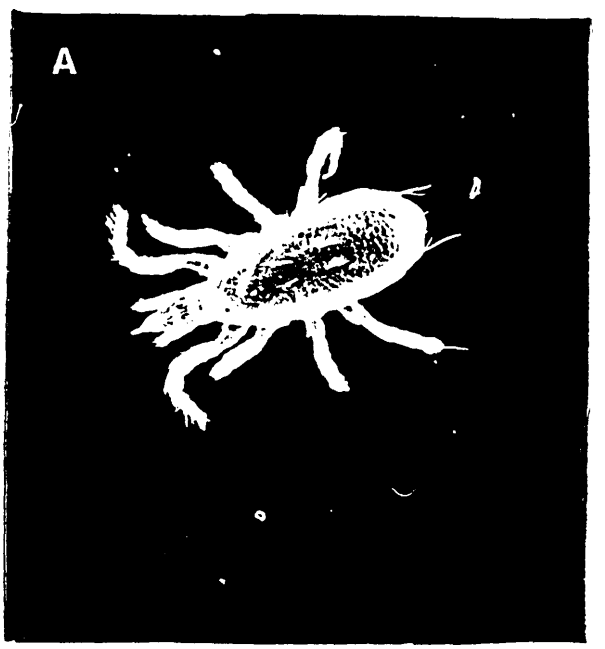
5.2 Materials and Methods

5.2.1 The Plants

The youngest fully expanded leaf (3rd from the top) on 2 month old plants was used as the experimental release site.

5.2.2 The Neoseiulus age-groups

Cohorts of adult females and nymphs were used. Each cohort was started from eggs laid over a 24 hour period. Each group was raised using the McMurtry-Scriven method for rearing phytoseiids. The basic unit was a petri-dish containing rubber foam saturated with deionized water which formed the support for a 8x8 cm rubber tile. The rubber tile served as an artificial substrate. Thin wisps of cotton were placed near the corners of the tile held in place by microslide cover slips. The wisps served as oviposition sites. Food, in the form of eggs of tetranychid mites, was placed in the middle. One hundred ovipositing Neoseiulus females were introduced to the unit and were removed 24 hours later. The rearing units were maintained in a conviron at 27°C and 60-70% r.h. Development was observed from egg to the correct stage needed for the experiment. There were 5 rearing units for each age-group. In order to synchronize adult and nymphal stages, the eggs for the two groups were staggered by a few days in their production. Plates 2A and B respectively show a deutonymph and an adult N. idaeus.



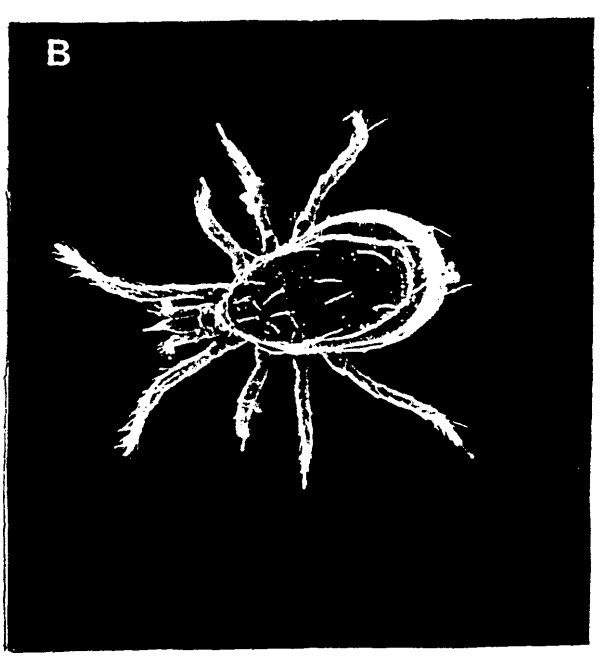


Plate 2. A deutonymph (A) and an adult Neoseiulus idaeus (B) (Magnification X100)

5.2.3 Experimental details

There were four densities for each age group: 25, 15, 10 and 5. Individuals of each group were first placed on clean 15 mm diameter cassava discs resting on wet tissue paper in petri-dishes. These discs were then pasted onto the adaxial surface of the experimental leaves using rubber paste which was easy to remove when dried. A day before the introduction of the phytoseiids 50 ovipositing CGM females were released onto each experimental leaf except on the control plants which were without prey.

There were 10 replicates for each density and for the control plants. Ten individuals of each phytoseiid group were used for the control. The experiment was conducted in the glasshouse at 28.5°C mean temperature and 66% mean r.h.

5.2.4 Experimental design

Complete randomization.

5.2.5 Data collected

Number of phytoseiids remaining 24 hours after their introduction.

5.2.6 Data analysis

Proportion of individuals of each age-group which remained were compared between the groups and between the densities using t-tests and analyses of variance.

5.3 Results

5.3.1 Emigration within age-groups

The percentage of adult Neoseiulus females which left the leaves

within 24 hours from each density was significantly greater than that which remained (P 0.005). The percentage remaining however did not differ between the densities (Table 57).

The proportion of nymphs that emigrated was significantly greater at densities 25 and 15 but did not differ from that which remained at densities 10 and 5 (Table 57). The percentage of nymphs which remained therefore tended to be higher at the lower than at the higher densities, although the mean number from the highest and lowest densities were 5 and 3 individuals.

5.3.2 Emigration between groups

The percentage of emigrants of each age-group did not differ at the higher densities between the groups, but did differ at the lower densities (t-test, $P < 0.05$; and $P < 0.01$ respectively at 10 and 5 densities) (Table 58). The results suggest that adult females have a greater tendancy to disperse at lower densities than the nymphs.

5.4 Discussion

Emigration occurred from all age-groups at each density within 24 hours of introduction. However, the percentage of female emigrants did not differ between the densities suggesting that emigration occurs even when prey are in abundance.

The majority of nymphs left the leaves at the higher densities (15 and 25), although more remained at the lower densities (5 and 10). Intraspecific competition probably prompted the higher nymphal emigration at the higher densities. This might explain the lower percentage of emigrants at the lower densities than at the higher densities which was not shown by the adult females.

Table 57 Percentage of each N. idaeus age-group emigrating within 24 h from the leaf of introduction

N. idaeus age-group	Density	% Emigrated	t-value
Adult females	25	83.2±3.0 a	13.63**
	15	80.7±3.7 a	10.33**
	10	74.0±6.0 a	5.08**
	5	78.0±3.6 a	10.12**
Nymphs	25	80.8±2.1 a	16.62**
	15	70.0±4.7 a	5.73**
	10	50.0±7.2 b	0.06NS
	5	46.0±8.5 b	0.63NS
lsd 5%		0.74	

Means within the column followed by same letter did not differ significantly at the 5% level
** Comparison with non-migrant population significant at 1% (T 0.01, 18df = 2.88)
NS Not significant at the 5% level
Student's 't' values and lsd values are based on arc-sine transformed data
Each figure is a mean of 10 data

Table 58 Comparison of the percentage of emigrants of N. idaeus nymphs and adults at four densities

Density	% emigrants Age-groups Nymphs	Adult females	t value
25	80.8±2.1	83.2±3.0	0.59NS
15	70.0±4.7	80.7±3.7	1.71NS
10	50.0±7.2	74.0±6.0	2.60*
5	46.0±8.5	78.0±3.6	3.30**

*, ** Significant at 5% and 1% level respectively (T 0.05 and 0.01, 18df = 2.101 and 2.878 respectively)
NS = not significant at the 5% level
Student's 't' values are based on arc-sine transformed data
Each percentage is a mean of 10 data

Bernstein (1984) observed that the emigration rate of Phytoseiulus persimilis depended upon the prey density, and suggested that when both prey and predator densities increased such that the population of the two was maintained at the same ratio, the emigration rate of the predator remained fairly constant. In the absence of its prey, P. persimilis emigrated at the same rate at both high or low densities.

In the present study, in which the prey population was constant while that of the predator varied, the percentage of female emigrants did not differ between densities. If density was the factor which prompted dispersal, then higher percentage of individuals at the lower densities should have remained on the leaves, but this was not the case with females. The dispersal of all individuals of each group from leaves without prey confirm the observations of Bernstein (1984), who found that all P. persimilis females introduced onto experimental plants without prey left the plants within 4 hours of introduction.

5.5 Conclusion

All N. idaeus females and nymphs introduced to plants without their prey dispersed from the leaf of introduction within 24 hours of their introduction.

Even in the presence of prey, the majority of the female predators dispersed from all the densities studies, the percentage of emigrants not differing between densities.

The percentage of nymphs dispersing within the 24 hours was higher at the higher densities (15 and 25) whereas at the lower densities (5 and 10), roughly similar number remained as had left.

The influence of prey density on the rate of predator emigration was not investigated in the present study. Further studies into this aspect

are required, as these observations have importance under field conditions.

SECTION 6. EXPERIMENT 4.

EFFECT OF STARVATION ON THE ACTIVITY OF ADULT FEMALE NEOSEIULUS IDAEUS ON CASSAVA PLANTS.

SECTION 6

Effect of starvation on the activity of adult female Neoseiulus idaeus on cassava plants

6.1 Introduction

The searching for and location of prey by phytoseiids involves movement, and this is influenced by starvation and by environmental factors. A 24 hour starvation period stimulated Amblyseius largoensis (Muma) to more rapid searching movement but after being starved for 48 h, the average rate of movement had decreased by about 50% (Sandness and McMurtry, 1972; Blommers et al., 1977). The effect of starvation on the activities of other arthropod predators has been widely studied: coccinellids by Banks (1957) and Frazer and Gill (1981), chrysopids by Baumgaertner et al. (1981)and syrphids by, Leir and Barlow (1982). Both satiation and extended starvation caused reduced activity (Banks, 1957; Hagvar, 1973; Frazer and Gill, 1981). With increasing starvation, the predators either dispersed or concentrated on searching activity. Temperature and humidity also influenced these activities with phytoseiid predators (Penman & Chapman, 1980), who reported that N. fallacis (Garman) responded significantly more rapidly to increased temperature and humidity. On the other hand saturated humidity caused both P. persimilis and T. urticae to stop movement within 4 hours. At intermediate relative humidities, the activity of P. persimilis did not decline as much as that of its prey (Mori & Chant, 1966), although dry air caused both the predator and its prey to be quite active. Also found to influence the movement of some phytoseiids is the texture of the plant's surface (Rasmy et al., 1984).

The effect of starvation on the activity of N. idaeus is less known.

The present study investigates the effect of four starvation categories on the activity of N. idaeus females.

6.2 Materials and Methods

6.2.1 Phytoseiid cohorts

Ovipositing N. idaeus females from IITA Biological Control Programme were introduced to 5 two month old potted plants heavily infested with CGM at 5 females per plant. The F_1 adults were again transferred to 5 new heavily CGM infested plants at 2 females per plant. These were removed from the plants 24 hours later and the resultant young females of F_2 generation were used for the experiment.

6.2.2 Starvation categories

The N. idaeus females were separated into three groups of 5 individuals without food in vials covered with very fine nylon mesh for 12, 24 and 36 hours respectively. The control (zero starvation) group was left with the CGM on the plants. The vials were maintained in the laboratory at room temperature (26-27°C and 40-50% r.h.).

6.2.3 Experimental plants

One month old potted plants (Plate 1) with 5 to 6 leaves were used.

6.2.4 Experimental details

An individual female from each starvation period was introduced onto the adaxial surface of the third fully expanded leaf from the top. when this individual had moved to the abaxial surface, its movement was monitored for an hour with the aid of a mirror held under the leaf.

An assistant was present with a watch recording the time of each activity. The experiment was carried out in the laboratory at the

temperature and relative humidity as given above. There were 10 observations for each starvation period. The experiment was completed in 4 days, each starvation category being completed per day. To ensure that all phytoseiids in each starvation group observed in a day were starved for the same period of time, the individuals were separated into subgroups which differed for one hour in the time the starvation was started.

6.2.5 Data collected

Time of activity, transit time between leaves and the number of lobes/leaf visited were recorded during the one hour observation period. When a leaflet/leaf was visited more than once, each visit was counted.

6.2.6 Experimental design

Complete randomization.

6.2.7 Analysis of data

The data were analysed using one way analysis of variance and student's t-test.

6.3 Results

6.3.1 Time of phytoseiid activity

The proportion of time spent in moving by individuals of each starvation category did not differ between the different starvation categories (Table 59), suggesting that the mobility of N. idaeus females was not significantly affected when individuals remain without prey for as long as 36 hours.

Table 59 The proportion of time female N. idaeus spent moving during 1st hour of introduction at four starvation categories

Starvation period (h)	Proportion of time spent in moving	P value
0	0.87	**
12	0.82	**
24	0.88	**
36	0.87	**

** Comparison with number remaining, significant at 1% level, (P 0.01, 18df = 2.88)
Means within the column do not differ significantly at the 5% level, (lsd 5% =)

Table 60 Number of leaves and leaflets visited and the residence time on leaf by female N. idaeus under four starvation regimes.

	Starvation regimes (h) 0	12	24	36	lsd 5%
Leaflets	29.3±2.6 a	24.1±3.6 a	28.2±2.9 a	24.6±3.1 a	NS
Number of leaves	1.1±0.1 b	1.2±0.1 b	2.3±0.3 a	2.0±0.3 a	0.65
Residence time (min)	59.2±0.8 a	58.3±1.5 a	50.3±2.5 b	52.2±2.4 b	5.5

Means within a row followed by the same letter do not differ significantly at the 5% level

6.3.2 Leaflets and leaves visited

The number of lobes or leaflets visited did not differ between starvation categories. However, the number of leaves visited did differ ($P<0.005$), with the phytoseiids deprived of food for 24 and 36 hours visiting significantly more leaves than the less starved treatments.

6.3.3 Residence and transit time

The time individuals of each starvation category remained on the leaves differed between categories ($P<0.005$). Fully fed individuals and those starved for 12 hours, spent significantly greater time on the leaf than individuals starved for 24 and 36 hours (Table 60). The transit time taken from leaving a leaf to the time of reaching the next leaf was not clearly indicated at the lower period of starvation as only very few individuals from these categories visited more than one leaf. However the transit time spent by individuals starved for 24 and 36 hours was respectively 5.4 ± 0.4 and 6.8 ± 1.0 minutes and did not differ at the 5% level.

6.4 Discussion

The activity of N. idaeus females starved for 0, 12, 24 and 36 hours did not differ significantly between the starvation categories. All the individuals spent more time moving than resting. Other workers found that female Amblyseius largoensis starved beyond 48 hours reduced movement by about 50% (Sandness & McMurtry, 1972; Blommers et al., 1977). The 36 hour starvation period used here for N. idaeus was probably not long enough to affect their activity. It has been observed with insect predators that both satiation and extended starvation resulted in little activity of the predators (Banks, 1957; Hagvar, 1973; Frazer & Gill, 1981).

The present study indicated that even at the 36 hour starvation period, N. idaeus was as active as when in the presence of excess food. However, the number of leaves visited by individuals starved for the different categories did differ between the starvation categories ($P \ll 0.005$), with those starved for 24 and 36 hours visiting more leaves than those starved for shorter periods. It appears that the individuals which visited more leaves during the observation period, spent a significantly shorter time per leaf than those which visited fewer leaves at the same time. Although the number of leaflets or lobes visited did not differ between the starvation categories, it is likely that the phytoseiids starved for 24 h or more visited the same leaflets less frequently than those at the lower categories of starvation.

The transit time spent by individuals starved for 24 and 36 hours did not differ, probably because both groups visited a similar number of leaves. Individuals at the lower starvation categories remained more or less on the same leaves of introduction, and therefore the transit times between leaves was insignificant. Longer transit times would be disadvantageous, reducing the time of searching on the leaves where the prey are found. It is suggested that further studies in the searching behaviour of N. idaeus in the presence of its prey should be carried out.

6.5 Conclusion

1. Starvation periods of up to 36 hours did not seem to affect the proportion of time spent walking by individuals of N. idaeus at the different categories of starvation.

2. Starvation periods of 24 and 36 hours resulted in more leaves being visited than individuals at lower categories of starvation, and this could be due to the longer periods spent per leaf by individual at the lower categories than at the higher categories of starvation.

3. Movement between leaves was much less frequent for the shorter starvation categories.

Further studies of the activity of N. idaeus at longer starvation categories than the present study is necessary to cover the possible range of prey availability associated with the different seasons.

SECTION 7. EXPERIMENT 5.

MOVEMENT AND DISTRIBUTION OF NEOSEIULUS IDAEUS FEMALES WITHIN A CASSAVA PLANT.

SECTION 7

Movement and distribution of adult Neoseiulus idaeus females within a cassava plant

7.1 Introduction

Phytoseiid predators of tetranychid mites are found widely in low herbaceous vegetation, intermediate shrubby growth and arboreal situations (McMurtry et al., 1970), usually spending much of the time on the undersurface of the leaves. The movement and distribution of the phytoseiids tends to differ between species. For instance Typhlodormus caudiglans (Schuster) occurs more frequently on bark than on leaves (McMurtry et al., 1970).

Several factors may influence the phytoseiid distribution on plants including the physical structure of host plant (pubescence or glabrous leaves, prominent leaf veins) and prey distribution (Downing & Moilliet, 1967). For instance, P. persimilis is rarely found on leaves not infested with the prey. On the other hand, Amblyseius hibisci (Chant) tends to be more randomly distributed (Huffaker et al., 1970). McMurtry & Johnson (1966) reported that Typhlodromus occidentalis and Eseius hibisci (Chant) were found toward the inner part of their host plants for part of the season and did not fully exploit prey on the peripheral foliage of the tree where the prey density may be high. Studies made on four species of predators on cotton showed that the area of greatest activity of each predator corresponded with the location of the suitable host stages (Wilson & Gutierrez, 1980).

On cassava, where different species of tetranychid mites are distributed at different levels, several predators including E. hibisci

and Cecidomyiid larvae were found mainly at the lower leaves (Pena & Waddil, 1982). T. urticae and P. citri, which inhabit the lower and middle leaves, were therefore exposed to greater predation than M. caribbeanae, which feeds on the upper leaves. The distribution and movement of N. idaeus on cassava is less well known, and the present experiment was designed to determine the movement and distribution of this exotic predator on cassava.

7.2 Materials and Methods

7.2.1 The Plants

Three month old potted plants with 21 leaves were used.

7.2.2 Phytoseiid age-groups A cohort of female N. idaeus was started from eggs laid over a 24 hour period and reared under the McMurtry-Scriven method as described by Friese et al. (1987) (Section 5 above).

7.2.3 Experimental details

The plants were separated into three groups of 10. In the first group, the phytoseiids were introduced onto the third leaf from the top; in the second onto the middle leaf (number 11), while in the last group, the predators were introduced onto the bottom most leaf.

Three days before the introduction of the phytoseiids, 200 ovipositing CGM females were placed on 15 mm diameter leaf discs, and then transferred to the bottom most leaf of each experimental plant. The CGM distribution was determined forty-eight hours later. After a further twenty-four hours, 40 N. idaeus females were introduced onto the leaves of each experimental plant as specified above. The experiment was carried out in the glasshouse at an average temperature of 28.5°C and 60%

r.h. Counts of all phytoseiids were made 24 hours after their introduction.

7.2.4 Experimental design

Complete randomization with plant spaced 1.5 m apart.

7.2.5 Data collection

Number of infested leaves and numbers of both CGM and phytoseiids recovered on them.

7.2.6 Data analysis

The distribution of the phytoseiids and that of the CGM were both compared between the lower and the upper halves of the plant for each treatment using Student's t-test.

The number of phytoseiids remaining after 24 hours was compared between treatments using Analysis of Variance.

The distribution of the CGM and Phytoseiids was compared on the plants using Regression Analyses. The population on the lowermost and topmost leaves were discounted as the phytoseiids had accumulated on these leaves, probably in preparation for emigration.

7.3 Results

The population of the CGM on all the experimental plants was skewed toward the upper half of the plants (Table 61).

More than half of the phytoseiids released at each site of initial introduction dispersed off the plant within 24 hours (Table 62). However, significantly more phytoseiids left the plants when the releases were made on the bottom-most leaves than when they were made on either

Table 61 Comparison of % infested leaves and % CGM between the lower and the upper halves of the plants on which phytoseiids were introduced at different sites.

Leaf of initial phytoseiid release	Lower half	Upper half	t-value
Top			
% leaves infested	77.0±3.35	80.0±3.33	0.74NS
% CGM recovered	35.8±1.79	58.2±2.1	7.97**
Middle			
% leaves infested	75.0±3.73	86.8±2.0	2.80**
% CGM recovered	33.5±1.49	61.6±1.81	11.70**
Bottom			
% leaves infested	66.0±3.05	75.0±3.73	1.95NS
% CGM recovered	36.2±2.80	54.9±2.79	4.71**

** Significant at 1% level, t 0.01, 18df = 2.878
NS = Not significant at the 5% level
Student's 't' values are based on arc sine transformation

Table 62 Percentage of female N. idaeus remaining 24 hours after introduction onto the plants at different sites

Site of N. idaeus initial release	% remaining	P value
Top leaves	26.0±2.8 a	**
Middle leaves	28.3±3.5 a	**
Bottom leaves	11.7±2.6 b	**
lsd 5%	0.54	

** Comparison with the numbers emigrating significant at 1% level, (T 0.01, 18df = 2.878)
Means within the column followed by the same letter do not differ significantly at the 5% level
Student's 't' and lsd values are based on arc-sine transformed data

the top or middle leaves (Table 62). Figs. 16A, B and C show the distribution of the phytoseiids on the plants when the initial phytoseiid introductions were on top, middle and bottom-most leaves respectively while Figs 17 A, B and C show the distribution of the CGM on corresponding plants.

The distribution of the phytoseiids did not appear to differ between the lower half and the upper half of the plant when the releases were made on the top and the bottom most leaves. However, the population of the phytoseiids was higher ($P < 0.01$) on the lower half than that on the upper half when the releases were made on the middle leaf (Table 63).

A regression analysis relating the distribution of the CGM to that of the phytoseiids on each treatment (excluding the upper and lower-most leaves) has shown weak relationships with correlation coefficients $r = 0.46$; 0.066 and 0.378 for the top, middle and bottom release sites respectively.

Figs.18 A, B and C illustrate the correlation that exists between the distribution of the CGM and that of the phytoseiids from plants on which the initial releases were made on the top, middle and bottom leaves respectively.

Although the greater percentage of the phytoseiids dispersed within 24 hours of their release, the results have shown some evidence suggesting that releasing the phytoseiids on the top or middle leaf is more advantageous than releasing them on the bottom (Table 62).

7.4 Discussion

In all treatments, more than 70% of the N. idaeus dispersed within 24 hours of introduction. The highest percentage of emigrants was recorded on plants where the releases were made on the bottom-most

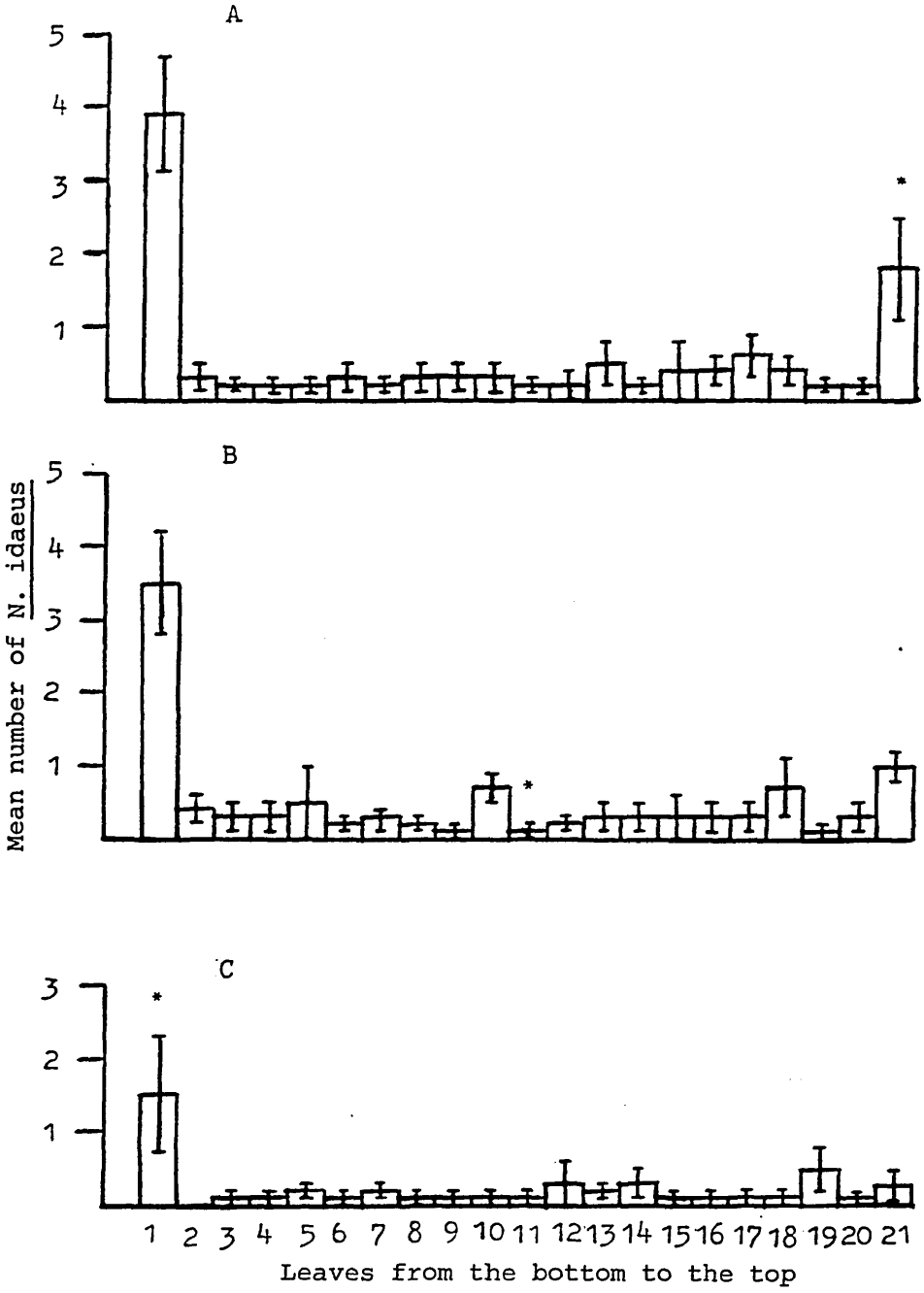


Fig. 16. Distribution of female N. idaeus on cassava plants 24 hours after introduction when initial introductions were made on (A) top, (B) middle and (C) bottom-most leaf

* Initial site of Phytoseiid introductions

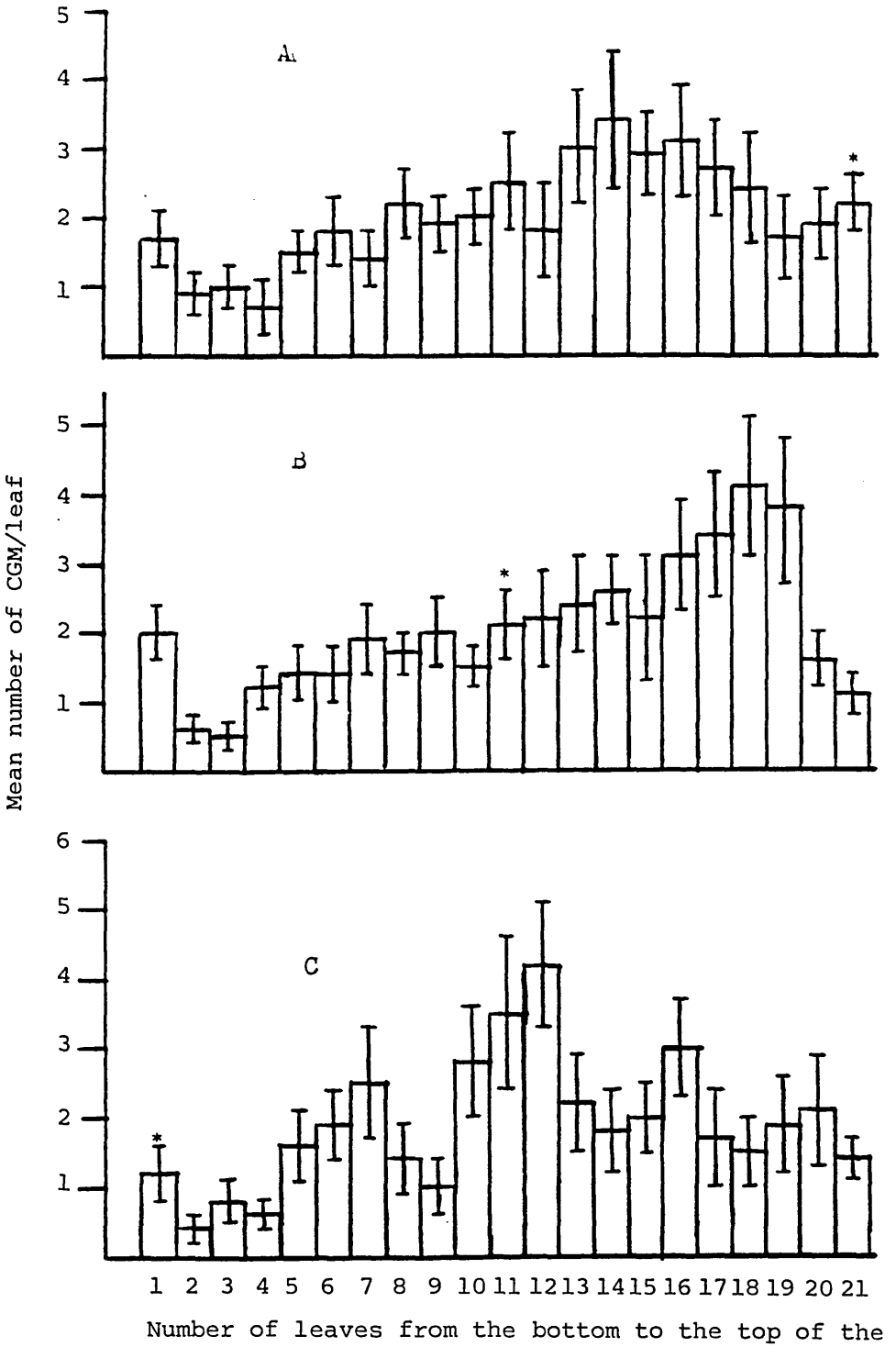


Fig. 17. Distribution of CGM on plants on which female N. idaeus were introduced on (A) top, (B) middle and (C) bottom-most leaf under glasshouse conditions

* Initial site of phytoseiid introduction

Table 63 Comparison of % infested leaves and % N. idaeus recovered between the lower and the upper halves of the plant for each site of initial phytoseiid release, 24 hours after the introduction

Leaf of initial phytoseiid release	Lower half	Upper half	t-value
Top			
% leaves infested	28.0±4.16	28.0±4.42	0.00NS
% N. idaeus recovered	55.8±5.61	41.6±5.40	1.71NS
Middle			
% leaves infested	36.0±3.71	29.0±6.20	1.10NS
% N. idaeus recovered	66.0±6.46	32.8±6.51	3.59**
Bottom			
% leaves infested	15.0±2.24	17.0±4.23	0.25NS
% N. idaeus recovered	56.2±8.29	43.0±8.38	0.84NS

** Significant at 1%, t 0.01, 18df = 2.787
NS = Not significant at the 5% level, t 0.05 18df = 2.101
Student's 't' values are based on arc sine transformation

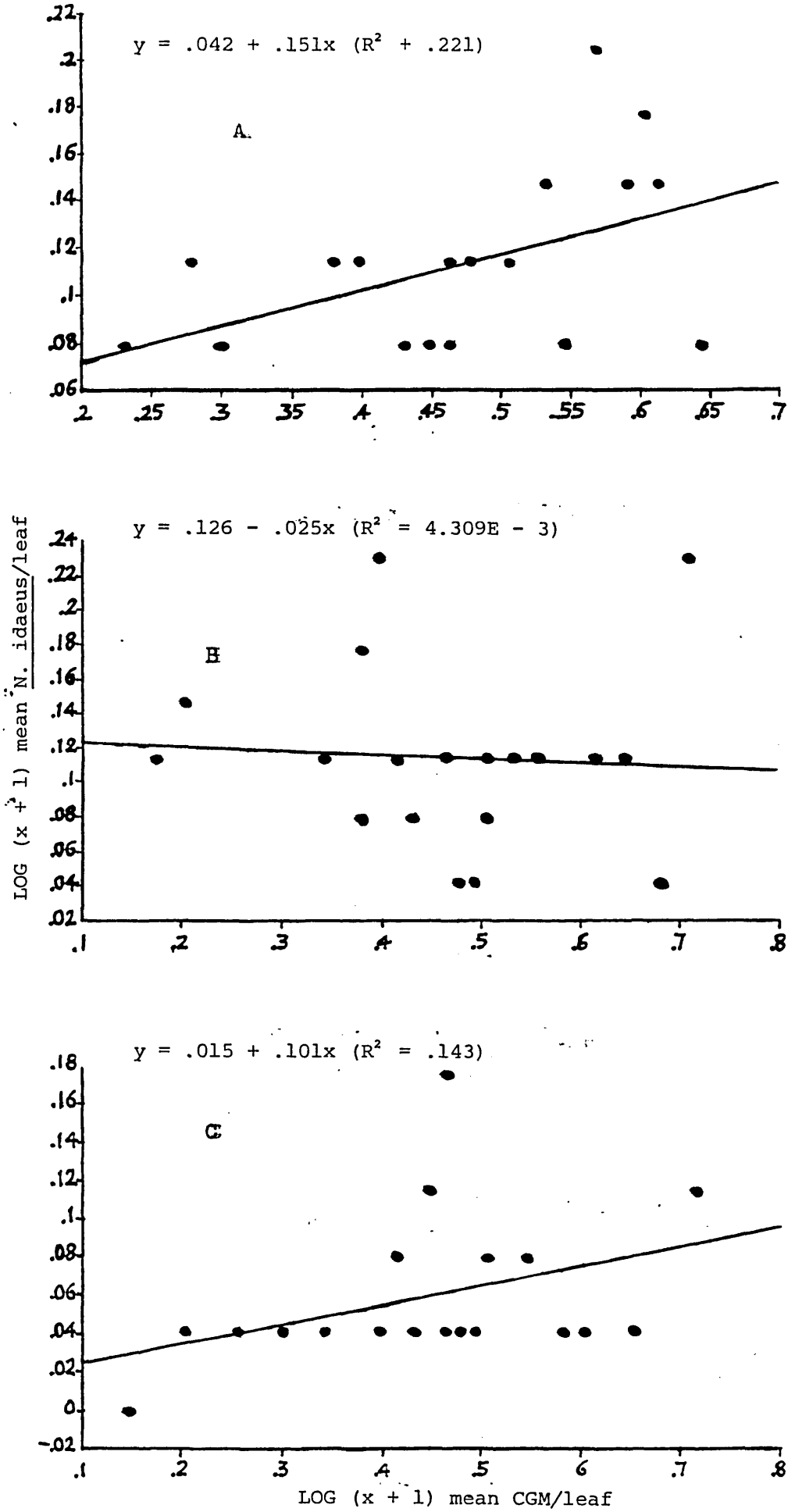


Fig. 18. Regression of the distribution of CGM on plant and of its phytoseiid predator N. idaeus released on (A) top, (B) middle and (C) bottom-most leaf 24 hours after introduction under glasshouse condition

leaves. The rapid dispersal of the majority of the phytoseiids from each plant might be due to more downward movement on the stem than that into the leaves where the prey are found.

Takafuji (1977) found that a decrease in prey prompted P. permilis to disperse, although he also noted that individuals dispersed quickly after their introduction, even on plants with sufficient prey.

In the present study, the prey did not appear to be a limiting factor despite their higher concentration on the upper half of the plant.

The high dispersal of the phytoseiids released from all sites on the plants raises a suspicion on the adaptability of the phytoseiids to the plant situation particularly that attributed to their searching ability.

7.5 Conclusion

Most of the phytoseiids released on the various sites on the plants dispersed off the plants within 24 hours of their release.

The distribution of the remaining phytoseiids released on the top and bottom leaves tended to be similar between the lower half and upper parts of the plants whilst that resulting from release made on the middle leaf was significantly greater on the lower half than that on the upper half of the plant.

However the correlation that resulted between the distribution of the CGM and that of the phytoseiids illustrated only a weak relationship for all the sites of phytoseiid release. Evidence based on percentage of phytoseiids recovered on the plants 24 hours following their release suggests that releases made on the top or the middle of the plants are more advantageous than releasing them on the bottom of the plants.

GENERAL CONCLUSION

1. Within the plant canopy, adult CGM stages tended to be the major emigrating groups from the leaves.

2. Mite density, leaf age, feeding by mites, the presence or absence of other mites and the presence of CGM slurry, all appeared to influence dispersal within the plant canopy.

3. The main emigration occurred within 6 h of the introduction. Little further significant emigration was observed with the adult groups in some treatments which appeared to suggest that settlement occurred within 6 hours of the introduction.

4. The distribution of all age groups was skewed toward the palm section of the leaf. Factors which contributed to this distribution were not studied in the present work. Further studies are necessary to determine whether or not nutritional or factors associated with protection were involved in this distribution.

5. More adult female CGM distributed on the upper half of the plant than on the lower half. Such preference was demonstrated by significantly more movement of the mites from the bottom or middle leaves than that down the plant from the top or middle leaves.

6. Both adult female and deutonymph N. idaeus emigrated within the plant canopy in the absence of their prey. However in the presence of their prey, the emigration of adult females was independent of their densities whilst that of the deutonymphs appeared to decrease with decreasing densities. Future studies should consider the effect of prey densities on the emigration behaviour of the phytoseiids.

7. Starvation periods from 0 to 36 hours did not appear to affect the

activity of female N. idaeus.

8. The distribution of female N. idaeus on the plant within the first 24 hours of their release did not differ between the upper and the lower portions of the plant whether the phytoseiids were released on the top or bottom leaves of the plants. However more than 70% of the phytoseiids released from any site on the plant left within 24 hours of their release. The weak relationship between the CGM distribution and that of the N. idaeus coupled with the rapid dispersal of the phytoseiids raised suspicion on the searching ability of the predator. Future attention should be given to the searching capability of N. idaeus and their dispersal between plants.

9. The effect of CGM slurry on the behaviour of N. idaeus was not studied in the present work. Future investigations would be worthwhile to determine whether or not the slurry could encourage longer retention of the phytoseiids on the plant.

10. Differences observed in the present work between lobes in the distribution of CGM suggested that future censuses should take into consideration all the lobes rather than extrapolating mite densities from selected lobes only.

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Appendix 1 Temperature and relative humidity under glasshouse conditions

Day	Temperature (°C) Min	Max	Relative humidity (%) Min	Max
1	23.5	35	57	99
2	22	34.5	58	99
3	23.5	33.5	56	96
4	24	32	58	99

Appendix 2 Weather record under field conditions

		Day 1	2	3	4
Rainfall		0	0	0	0
Evaporation		5.8	4.42	4.29	4.25
Wind speed miles/h		4.8	5.7	4.8	3.7
Solar radiation Gm-cal/cm2/day		-	525.17	389.64	423.53
Temperature (°C)	Min	24.6	24.8	25.3	24.9
	Max	34.0	34.6	31.4	32.9
Relative humidity (%)	Min	47	45	62	56
	Max	73	72	80	75

Source: IITA Weather Record Station 1988.