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GENETIC INCOMPATIBILITIES AMONG POPULATIONS OF CASSAVA GREEN MITE COMPLEX *MONONYCHELLUS SPP.* (ACARI:TETRANYCHIDAE) AND THEIR IMPLICATION IN THE TAXONOMY OF THE MITE

BY

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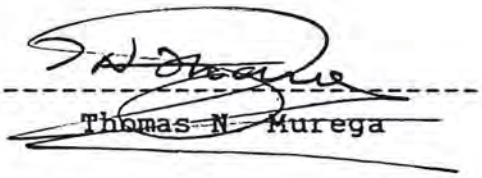
QUOTATION

"The fate of empires depend on the education of the youth"

Aristotle (383-322 BC)

DECLARATION

This thesis is my work and has not been presented for a degree in any other University.



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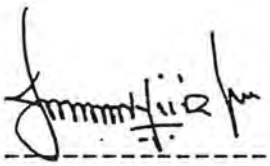

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DEDICATION

To

Tabitha, George and Ruth
plus the youth of this world that
they by emulating us may build a
better tomorrow

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ABSTRACT

Hybridization tests revealed various levels of reproductive isolation among 19 populations tested. Mean egg lethality was highest in the F_2 than in the F_1 and F_3 ($F_1 < F_2 > F_3$; $p<0.0003$). Populations from Nyanza, Western and Coast had higher lethalities compared to those from Central Kenya (mean lethality =11.69, 9.26 and 6.35%, respectively). Sub-specific populational differences were recorded on populations from Central Kenya ($p<0.05$) compared to other sites ($p=>0.05$). However intra-populational check crosses revealed that these differences were not due to gene interaction but resulted from heterogeneity as a result of extra-chromosomal factors ($p<0.05$) in the different setal morphs. This is evidenced by successful zygote formation and therefore, a common gene pool is shared.

Hybrid success of the susequent progenies indicated absence of hybrid sterility, inviability and, or breakdown and distorted sex-ratios (range=1:1-8:1). Preponderance of diploid offspring indicated fertilization was successful among all the populations hybridized. The arrhenotokous mode of reproductive parthenogenesis was demonstrated which gave an exclusive haploid

male progeny from uninseminated virgin females..

Based on the shape of their aedeagii, all the males from the six sites were identified as *Mononychellus progresivus* while the 6 females were classified as short, long or intermediate setaed parents (range= 20.02-45.76 μm). The 6 F_1 generation lines crossed segregated into distinguishable short, long and intermediate setal forms (range=17.56-33.24 μm). The D_1, D_2 and D_3 setae increased with body size (r=0.877, 0.97 and 0.93, respectively; $p<0.0001$), but were different in each of the 6 sites ($p<0.0001$). The existence of the three setal morphs suggested that setae inheritance is polygenic and is controlled by three non-allelic genes. Because of their great variability, the dorsal setae cannot, therefore, be reliably used for species diagnosis. The shape of the aedeagus was found to be the only reliable morphological species diagnostic tool due to its genetic stability.

It is questioned whether *M. tanajoa* and *M. progresivus* are discreet species. The weight of the evidence justifies the conclusion that *M. tanajoa* and *M. progresivus* are one and the same species.

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1.0 GENERAL INTRODUCTION

The origin of the cassava plant, *Manihot esculenta* Crantz (=*Manihot utilissima*), family Euphorbaceae, is neotropical in N. E. Brazil and the savannahs of Central America especially Venezuela (Rogers, 1963). It was introduced by the Portuguese (Montaldo, 1973) into West Africa through the gulf of Benin and the Congo basin in the second half of the 16th century and into East Africa through Reunion, Madagascar and Zanzibar at the end of the 18th century (Jones, 1950; Agboola, 1968; Jennings, 1970).

Today cassava is grown in in 34 countries in the sub-Saharan Africa between the latitudes 30°N and 30°S at elevations ranging from sea level to about 2000 m (Jones, 1959; Martin, 1970) and accounts for 44% of the total world production (Herren, 1987). Tubers are an important source of dietery carbohydrates (Kirkby, 1984), supplying calories for over 200 million people in the sub-saharan region (IITA, 1985), while leaves provide proteins and vitamins (Herren, 1987). It can thrive in exhausted soils of the marginal arid and semi-arid areas of the tropics (Herren and Bennett, 1984). The productivity of cassava is higher per unit land per time (250 kcal/ha./day)

than rice (176), maize (200), sorghum (114) and wheat (110) (Coursey and Haynes, 1970). Cassava is used for a variety of purposes including food substitutes (Coursey and Booth, 1978), starch, adhesives, explosives, dyes, linoleum, livestock feed (Burger, 1952; Flaws and Palma, 1968, Lima, 1977; Li and Chang, 1978) and power alcohol (Coursey and Booth, 1978).

Unfortunately, the cassava plant is plagued by various pests (chiefly the cassava green spider mite (CGM) and the cassava mealy bug (CMB) and diseases (mainly the African cassava mosaic (ACM) (Belloti and Schoonhoven, 1978). Severe infestation by the CGM results in yellow chlorotic spots resembling the ACM symptoms (Byrne *et al.*, 1983). Severe infestation may give rise to complete defoliation (Nestel, 1976), resulting in reduced root size and poor tuber formation (Nyiira, 1982). In Africa, tuber losses resulting from the feeding activities of the CGM is estimated to be as high as 80% worth a colossal US $ 1.8 billion (Herren, 1978).

The first CGM infestation in Africa was reported near Kampala, Uganda by Nyiira (1972) and Lyon (1973). The CGM spread and dispersal in Africa is thought to have occured mainly through infested cassava cuttings from S. America (Murphy,

1984). The spread outwards is enhanced through the free movement of planting material and the presence of susceptible cultivars (Herren, 1987). Other methods of spread are believed to be passive wind dispersal (Megevand *et al.*, 1987) and through phoresy (Belloti and Schoonhoven, 1978).

As at 1971, the genus *Mononychellus* was only known to contain 17 species, 4 of which viz. *M. bondari* Paschoal, 1970, *M. caribbeanae* McGgregor, 1950, *M. planki* (McGregor, 1950), Paschoal, 1971, and *M. tanajoa* (Bondar, 1938), Flechtmann and Baker, 1970 occurred in different S. America countries (Gutierrez, 1987). The Ugandan specimens were identified as *M. tanajoa* as were all other subsequent specimens collected elsewhere in Africa until the discovery by Flechtmann in 1982, of another species *M. progresivus* Doreste 1981 from Gabon and Nigeria. The existence of the two CGM species in Africa has created a lot of confusion among various workers who who have tried unsuccessfully to define the two by comparing the the length of the dorso-central setae in relation to their longitudinal distances from each other (MacFarlane, 1984, Gutierrez, 1987; Rogo et *al.*, 1987).

The confusion surrounding the taxonomic identity of the CGM in Africa started when Bondar

(1938), described the first CGM in the type region of Bahia in Brazil as *Tetranychus tanajoa* based on female specimens only. Subsequent reference to this type specimen has been impossible as the original slide was lost. This and other *Mononychellus* species infesting *Manihot* species in S. America have subsequently had their names changed over the years (Pritchard and Baker, 1955; Wainstein 1960, 1971).

Flechtmann and Baker (1970) collected from the Bahia type region females which resembled Bondar's *Tetranychus tanajoa* but which they redescribed as *Mononychus tanajoa*. They based their description on the reticulations of the female's prodorsum, striation patterns of the opisthosoma and the length as well as the position of the dorso-central hysterosomal setae (the D_1, D_2 and D_3) in relation to their longitudinal distances from each other. However, Wanstein (1971), found the genus *Mononychus* to be preoccupied and consequently relocated it to the genus *Mononychellus*. From the same Bahia material, they also described *Mononychellus planki* which they split into *M. planki sensu stricto* McGregor 1950 and *M. mcgregori* Flechtmann and Baker 1970. The latter was also reported by Urueta (1975) from Colombia. From Brazil, Paschoal (1971), also

identified *M. planki*.

Based on the material he collected from Venezuela, Doreste (1979), reported *M. astradai* Baker and Pritchard, 1953 and in 1981 he described two new species, *M. manihoti* Doreste, 1981 and *M. progresivus* from the same plant. In 1982, he added *M. chemosetosus* Paschoal, 1970 and *M. tanajoa*.

A total of 8 *Mononychellus* species have been described from alternative host plants other than cassava (Tuttle and Baker, 1968; Meyer, 1974, Tuttle *et al.*, 1974). Based on all available evidence, the genus *Mononychellus* now appears to contain a total of 27 species (Gutierrez, 1987) which infest cassava world-wide. However, only 8 have been identified from cassava in S. America, the native home of the cassava (Gutierrez, 1987). These are: *M. bondari*, *M. carribeanae*, *M. chemosetosus*, *M. astradai*, *M. manihoti*, *M. mcgregori*, *M. progresivus* and *M. tanajoa*). However, Gutierrez (1987), believes *M. astradai* and *M. chemosetosus*, to be synonyms of *M. tanajoa* while *M. planki sensu stricto*, is a synonym of *M. mcgregori* due to the similarities between these species in the striations of the female dorsum.

The controversy of the validity of 2 species attacking cassava in Africa is further compounded by the fact that out of the 8 species

reported attacking cassava in S. America, only two have been documented in Africa. Current thinking is that perhaps this confusion came about due to the morphological approach adopted in CGM species identification. For example, the length and the position of the dorsal setae, the standard morphological criteria used in species distinction varies tremendously from one strain to another and even between specimens of the same strain (Gutierrez, 1987).

Based on the above facts, it is clear that the status of our knowledge on the exact taxonomic identity of the cassava green mite is scanty and confusing. Previous treatises were largely based on the morphology of the female prodorsum setae (Flechtmann, 1978, 1982). The use of the male terminalium as an important species diagnostic tool was previously ignored, although Ewing had recognized its usefulness as early as 1913.

Re-examination of most of the original type specimens from S. America have shown that the D_1-D_3 setae as well as the tibia counts could not diffentiate *M. tanajoa* from *M. progresivus* (Gutierrez, 1987; Rogo *et al.*, 1987). Furthermore, considerable overlap occurs in delineating these setal forms so that they seem to range from short

to long in a continuous gradient. In between the short and the long are intermediate setal forms (Rogo *et al.*, 1987). The three allopatric morphs share the same ecological requirements and interbreed freely (Murega, 1989).

Further re-examination of the African specimens seems to indicate that *M. tanajoa* does not occur and only the composite *M. progresivus* does (Rogo *et al.*, 1987). Since the chaetotaxy of the CGM females has been shown to be genetically unstable, the presence of *M. progresivus* can only be confirmed morphologically by examining the profile of their genetically stable haploid sons. Since 8 species are known to be present in S. America (Gurtierrez, 1987) from where cassava was introduced from (Montaldo, 1973), the question of the occurrence of 1 or 2 CGM species in Africa is perplexing. Although it is speculative to state that the S. American CGM species were also misidentified, perhaps such a notion should not be ruled out.

There is need for a critical revisionary study of the taxonomy of the whole CGM complex as the urgency to apply classical biological control intensifies. Due to this urgency and the failure of morphological techniques to resolve the CGM identity, it was found imperative to use other

diagnostic methods in a bid to unravel the apparent mystery and confusion sorrounding the taxonomy of this apparently polytypic species.

The magnitude and urgency of the problem has mobilised efforts from international research institutes, donor organizations, the OAU and participating governments to form a co-ordinating body, the Africa-wide biological control programme of cassava pests (ABCP), in a bid to control the CMB and CGM (Herren, 1982, 1983). The ideal CGM management strategy is biological control using exotic predators from S. America, the type region from where the CGM was originally introduced (Terry *et al.*, 1980; Yaninek *et al.*, 1987). The red spider mites (RSM) cause little significant damage because of the activities of locally adapted predators and probably the high cyanide content in the plant (Belloti and Schoonhoven, 1978). However, this RSM natural enemy complex has failed to control. Often, local natural enemies do not control exotic pests (Matile-Ferrero, 1977, 1978; Nwanze, 1978; Girling *et al.*, 1977). This is because the former have not evolved with their hosts but have merely "switched over" from related hosts (Doutt and deBach, 1964).

For successful biological control, as stated earlier, the precise taxonomic status of

the target pest is crucial as efficient predators are specific to their prey (Schelinger and Doutt, 1964). Misidentification of the target pest can lead to fruitless introduction of the wrong natural enemy, a waste of effort and money (Kumar, 1984). To safeguard against failures of biological control efforts, it is crucial to correctly identify the CGM whose taxonomic identity has been in question for a long time (Doreste, 1981; Flechtmann, 1982; MacFarlane, 1984; Gutierrez, 1987; Rogo *et al.*, 1987; Murega, 1989).

According to current scientific evidence, only closely related spider mites hybridize. Members of different species do not form viable hybrid zygotes due to either pre-zygotic (pre-mating barriers viz. mechanical, spatial, behavioural and ecological), or post-zygotic (genetic and/or cytoplasmic incompatibility) isolation mechanisms (de Boer, 1985). In the latter case, either hybrid sterility, hybrid inviability or hybrid breakdown ensures that defective hybrid zygotes do not form beyond the F_1 generation.

For these reasons, it was felt that a different approach to the problem of CGM taxonomy using hybridization and genetic isolation studies was necessary to resolve the current taxonomic

confusion of the CGM. This is the first time genetics are being used to solve the CGM identity crisis although similar techniques have been used on other spider mites of the Tetranychidae family notably, the Tetranychus urticae group (Helle and Pieterse, 1965) *T. cinnabarinus* (Jordaan, 1977) and *T. neocalodenicus* complex (Gutierrez and van Zon, 1973).

The objectives of the present studies are as follows:

1. To test the level of conspecificity of the various CGM populations present in Kenya in order to establish the magnitude of inter-populational compatibility.

2. To asses egg lethality values so as to establish the presence or absence of intra-populational compatibility

3. To conduct sex inheritance and sex ratio studies in order to confirm existence of arrhenotoky and any underlying genetic abnormalities.

4. To establish the mechanism of genetic inheritance of dorso-central hysterosomal setae

used by morphologists to designate the CGM species.

2.0 LITERATURE REVIEW

2.1 Spider mite taxonomy.

The spider mites belong to the phylum arthropoda, the class Arachnida, sub-class Acari and order Prostigmata. spider mites lack conspicuous body segmentation, mandibles and antennae, and except in the larvae which has three pairs of legs, adults have 4 pairs (Berlese, 1897; Oudemans, 1897; Reck, 1952; Baker and Pritchard, 1960). Four families are regarded to be of agricultural importance: the Tetranychidae Donnadieu are the most important (Pritchard and Baker, 1955). This family is sub-divided into the sub-families Tetranychinae, tribe Tetranychini (the true spider mites) infesting higher plants and the Bryobinae which infest grasses and low growing plants (Krantz, 1978). Other families are the Tenuipalpidae (the false spider mites), the Tuckerellidae (the peacock mites) and the Eriophidae (the gall mites) (Baker and Pritchard, 1953).

2.2 Taxonomy of Tetranychidae Donadieu

This family with about 450 species (Krantz, 1978) consists of two important genera, *Tetranychus* Berlese comprised of the red spider mite complex and *Mononychellus* Wanstein, the cassava green mites (Tuttle and Baker, 1968; Flechtmann and Baker, 1970; Meyer 1974; Doreste, 1981; MacFarlane, 1984).

The taxonomy of Tetranychidae has undergone considerable metamorphosis since Donnadieu assigned them this supragenic name in 1875. Since then several other classifications have been proposed (Murray, 1877; Berlese, 1897; Oudemans, 1897; Reck, 1952). Baker and Pritchard (1953), gave a comprehensive family list consisting of two sub-families the Bryobinae and the Tetranychinae. Subsequent publications have maintained these sub-divisions (Pritchard and Baker, 1955; Meyer, 1974). The classification of Reck (1952, 1859), Mitrofanov (1972, 1977), assigning the two sub-groups family status have been rejected (Lindquist, 1985)

The Tetranychid mites are distinguished from mites of other families by the presence of a stylophore (fused basal segments of the chelicerae), a "claw" (fourth palpal segment) and

the presence of not more than 16 pairs of body setae (Pritchard and Baker, 1955). These setae can be of three types, sensory or tactile (found on the general body surface), or tenent hairs (found on tarsal appendages). On tarsal segments are some intimately associated setae, the "duplex setae" which occur as a pair. One setae occuring distally is sensory, while the proximal one is tactile. The dorsum of tarsus I and II consist of two and one pair of these "duplex" setae respectively. Also occuring on the tarsal appendenges laterad to the empodium are a pair of true claws. These and the tarsal "duplex" setae are useful in distinguishing species groups or higher taxa. Sensory setae occur on all tarsal appendenges, the anterior tibia and occassionally tibia II to IV, other setae on all appendenges are tactile. On the female opisthosoma are irregular or widely spaced striae or integumentary folds which bear finger print-like patterns. Viewed from the venter, the folds occur between the genitals and the post-genital setae. These are species specific and are useful complimentary taxonomic tools (Pritchard and Baker, 1955; Boudreaux, 1956).

At the generic or tribal levels, the chaetotaxy of the females' hysterosoma are used to distinguish these taxa. In Tetranychinae Berlese,

the idiosomal setae are such that the propodorsoma (proterosoma) bears 3 pairs, the P_1, P_2 and P_3, the metapodosoma and the opisthosoma (hysterosoma), 5 pairs of dorso-central D_1, D_2, D_3, D_3, D_4 and D_5 setae, 5 pairs of lateral L_1, L_2, L_3, and L_4 setae, and 1 pair of humeral setae the H, laterad to the D's (Gutierrez, 1985).

The D_1, D_2 and D_3 (used in CGM taxonomy) are referred to as dorso-central hysterosomals, the D_4 and L_4 as the inner and outer sacrals and the D_5 as the clunals (Gutierrez, 1985). An alternative classification, names the P_1 as the parietals, the P_2 and P_3 as the oculars, the D_1, L_1 and H as the scapulars, the D_2 and the L_2 as the prelumbals, the D_3 and L_3 as the lumbals, the D_4 and L_4 as the sacrals and the D_5 as the caudals (Reck, 1959, Mitrofanov, 1971).

The ventral surface setae are not as important as idiosomal setae in taxonomy. However, they are constant within the family except in the opisthosoma (Pritchard and Baker, 1955). In females, there are 3 pairs of medio-ventral setae (Mv_1, Mv_2 and Mv_3). The anal setae bears 1 pair of pregenitals (PrG), 1 pair of genitals (G), 1 pair of post-genitals (PoG), 2 pairs of anals and 1 pair each of the anterior and the posterior para-anals. Males have 4 pairs of genital-anal setae

(Reck, 1959; Wanstein, 1960) (Fig., 25)

2.3 The CGM identity crisis.

Mononychellus Wanstein is distinguished by the presence of dorsal reticulations between the two 3rd dorsal hysterosomal setae, two pairs of para-anal setae, proximity to each other of the duplex setae on tarsus I and II, 3 pairs of proximo-ventral setae on the empodium, and the body setae being borne on weak tubercules (Smith Meyer, 1974; Wanstein, 1971; Tuttle *et al.*, 1974).

At the species level, distinction between *M. tanajoa* and *M. progresivus* whose identity is in dispute, and which both reportedly attack cassava in Africa, is based on body setae and the profile of the aedeagii (Doreste, 1981). *M. tanajoa* is described as having short strong setae consisting of 9 tactile setae and one slender solenidion on tibia I, 7 tactile setae on tibia II and 5 proximal tactile setae and 1 solenidion and 3 tactile setae and 1 solenidion on tarsus I and II respectively. In *M. progresivus*, the setae are long, comprised of 8 tactile setae and 1 solenidion on tibia I and 4 proximal tactile setae and 1 solenidion on tarsus I.

The primary structure of the aedeagus is

a shaft and a knob, the latter may or may not be engrossed by secondary structures. In *M. tanajoa*, the teminalium is strong and straight ending in a bulging knob with two projections directed sharply towards its basal part while in *M. progresivus*, the aedeagus consists of a simple knob with no strong ventral hook (Doreste, 1981; MacFarlane, 1984) (Fig. 31, Plate 8). The male's terminalium and the female's genitalia are a critical lock-and-key system (Gutierrez, 1985). This species-specific system acts as a pre-zygotic mechanical mating barrier among spider mites of different species.

Bob-manuel (1987), studied the entogeny of the CGM body setae in all CGM instars and adult females and subjected them to principal component analysis (PCA), cluster analysis and other tests. The scatter plots of the operational taxonomic units (OTU'S) of the instars and adult females showed that only one species was present. Using iso-electric focussing and cuticular hydrocarbon studies of the CGM iso-enzymes, consisting of 13 enzyme/substrate systems, Oyugi (1989), found that there was no biochemical variants of CGM populationsin Kenya and, therefore, no evidence could be adduced to show that more than one CGM species occurred.

2.4 Genetic compatibility data in taxonomy.

The acarina which includes ticks and mites are the second important group of arthropods after the insecta (Oliver, 1965). Compared to the insecta, the genetics of the acarina is not well studied due to lack of standardized techniques (Balashov, 1979). The few references available concern acaricide resistance, cytogenetics and population genetics (Balashov, 1979). The study of the latter is hampered by lack of visible genetic markers (Balantyne, 1969; Balashov, 1979; Helle, 1985). Among spider mites, very few markers have been been identified (van Zon and Helle, 1966). The most investigated species is the *Tetranychus urticae* complex and *T. pacificus* because of the presence of good genetic markers which facilitate elucidation of the mechanism of inheritance within the haplo-diploid system. (Helle and van Zon, 1970; Helle and Pijnacker, 1985). Like in ticks (Balashov, 1979), no genetic markers have been ivestigated in *Mononychellus*. In such cases the structure of the genotype can only be determined from the sum total of their phenotypic expression (Balashov, 1971) and thus the composition of the

genotype is poorly defined (Balashov, 1982).

In ticks, taxonomic and phylogenetic relationships between various taxa such as *Dermacentor* x *Boophilus*, *Hyalomma* x *Rhipicephalus* and various strains of the *Ornithodorus* species complex has been clarified through genome incompatibility (Pervomaisky, 1951, 1959; Cwilich and Hadani, 1963, 1966). Incompatibility in the F_1 varied from complete sterility in *O. verrucoccus* x *O. papillipes* and *O. verrucoccus* x *O. tartakovskyi* to partial sterility in *O. pallipes* x *O. tartakovskyi* and *O. nerensis* x *O. alactagalis* (Graham et *al.*, 1972; Oliver et *al.*, 1972). Intraspecific differentiation among spider mites is easily studied by means of check crosses (de Boer, 1985). In ticks this has been studied on *O. tartakovskyi* and *O. verrucoccus* (Balashov, 1971). A phenomenon akin to that reported by de Boer (1980, 1981) among Dutch and Belgian populations of *T. urticae* complex was also reported among *O. verrucoccus* and *O. tartakovskyi* ticks by Balashov (1971). Partial to complete sterility was detected, in addition, introgressive hybrids occurred in the tick populations from two extreme ends of the test area. Similar introgressive hybrid swarms were reported by Dosse and Boudreaux (1963) when a laboratory maintained acaricide

resistant and a non-resistant strain of *T. urticae* were contaminated with *T. telarius*. In ticks and spider mites it has been shown that sterility barriers broke down when several intra-fertile clines were hybridized after several generations in the laboratory. This implied that genotypic differentiation had not become irreversible yet and the partial sterility was due to spatial isolation (Balashov, 1981; de Boer, 1980, 1981). Both inter- and intra-strain partial sterility is a feature common in most spider mite species where some form of partial lethality is found virtually between any two spider mite strains (Boudreaux, 1963; de Boer, 1980). Helle and Pieterse (1965) attributed intra-population lethality to heterogeneity in colony composition. High inter-strain F_1 lethality in diploid eggs showing shift in sex ratio in favour of males was demonstrated by Helle and Overmeer (1973) among populations of *T. urticae* complex. F_1 hybrid sterility does not depend on geographical separation since sympatric populations with the same morphological configuration can result in complete hybrid break down while allopatric ones can give viable progeny (de Boer, 1980).

In spider mites reproductive data has been used before to clarify taxonomic status among

species whose identity has been disputed (van de Bund and Helle, 1960). The demonstration of reproductive isolation between various species has helped in the unravelling of taxonomic status of several spider mite species (Dosse and Boudreaux, 1963). The identity of the following have been elucidated: *Paratetranychus citri* x *Panonychus citri* (Newcomer, 1928), *T. multisetis* x *T. bimaculatus* (Keh, 1952), *T. desertorum* x *T. bimaculatus* (Iglinsky and Rainwater, 1954), *T. pacificus* x *T. macdanieli* (Newcomer, 1954), *T. urticae* x *T. cinnabarinus* (Dosse and Langenscheidt, 1964; du Pont, 1979), *T urticae* X *T. telarius* (Keh, 1952; Boudreaux, 1956; van de Bund and Helle, 1960; Parr and Hussey, 1960, 1961), among different populations of same species in *T. neocalodenicus* (Gutierrez and van Zon, 1973), phytoseeid *Typhlodromus occidentalis* (Croft, 1970), *T. urticae* complex (Boudereaux, 1963; de Boer, 1979, 1980, 1983; de Boer and Veerman, 1983; Helle and Pieterse, 1965; Helle and van de Bund, 1962; Overmeer and van Zon, 1976), *T. telarius* (Dillon, 1958; Ghobrial et al., 1969), *Panonychus citri* (Inoue, 1977) and *T. cinnabarinus* (Jordaan, 1977). Such reproductive barriers have not been well studied in *Mononychellus* species complex. Only one reference on cross-breeding

studies on *Mononychellus* spp. from East Africa is available (Murega, 1989).

Boudreaux (1956), observed an extreme case of hybrid breakdown and inviability in a cross of *T. yusti x T. urticae* in which a single female was produced but soon died as a result of disharmonious gene recombination. Hybrid sterility was also reported by the same author between *T. telarius x T. urticae* from Lousiana whereby the hybrid produced small non-viable eggs, reciprocal crosses were not possible as genetic death ensued. In another experiment (Bouderaux, 1956), performed a mass cross between British *T. urticae x T. telarius*, 3 females laid no eggs, 2 produced 1 sterile female and 3 males while the rest produced 214 females and 529 males giving a distorted sex-ratio of 0.4:1 showing that a high mortality of diploid eggs occurred. Among such progeny females lay infertile eggs or no eggs at all. This prevents full segregation of genes, hampering phenotypic and genotypic expression. From this data he concluded that the two species were reproductively isolated and were thus separate species.

Reduced fertility or semi-compatibility was reported among offsprings of *T. telarius x T. urticae*, whereby fewer females and more males were

produced. The females were also observed to feed less (Monroe, 1963). When Dillon (1958) crossed red *T. telarius* x *T. bimaculatus*, eggs were produced but hatching failed to occur. He stated that when eggs fail to hatch, sterility is suspected but when siblings fail to reach maturity hybrid inviability and/or hybrid breakdown is the cause. Similar results were obtained by Boudreaux (1956), when he crossed green *T. telarius* from Lousiana x *T. cinnabarinus* from unknown source. The female siblings were very few and only a small percentage laid eggs most of which were sterile. The females which survived produced mainly males and females which were sterile showing that fertilization failed as the sexes were incompatible. The green *T. telarius* x red *T. urticae* crosses revealed intersterility barriers, a sign of absence of conspecificity.

Such hybrid sterility phenomenon was attributed to a non-mendelian factor in the cytoplasm causing incompatibility between the ovum and the sperm (de Boer, 1979). This maternally inherited sterility factor was postulated to be the cause of semi-sterility when strains of *T. urticae* complex were crossed (Overmeer and van Zon, 1976: de Boer and Oreel, 1980; de Boer and Veerman, 1983). Such lethality factors could also

be due to a single recessive gene passed through the daughters and not the sons but expressed in haploid males derived from crosses involving such recessive daughters (de Boer and Oreel, 1980). Heterosis in subsequent filial generations showed that the strains were of the same species because the partial sterility was only a transcient phenomenon. Similar conclusions were made earlier by du Pont (1979) from crosses between *T. urticae* Koch and *T. cinnabarinus* Boisd.

2.5 Sex inheritance and sex-ratio studies

The male producing parthogenesis or arrhenotoky is useful in the interpretation of hybridization data among haplo-diploid systems. Among the Acarina, the predominant mode of sex inheritance is arrhenotokous parthenogenesis and to a lesser extent the female producing thelytoky (Oliver, 1971; Helle and Pijnacker, 1985) but deuterotoky which produces both male and female haploid offspring although very rare occurs in some taxa (Whiting, 1945; Rieger *et al.*, 1976). Many workers use the term haploid-diploidy to mean a sex determining system whereby males are haploid and females diploid. Arrhenotoky, therefore, is a

haplo-diploidy sex mechanism in which males result from parthenogenesis. Others use the term parthenogenesis interchably with arrhenotoky to refer to the production of an all male haploid offspring, but haploid parthenogenesis can also result in haploid females (Pijnacker *et al.*, 1980). To avoid the above confusion "male haploidy" and "female haploidy" are preferred (Helle and Pijnacker, 1985). In some dermanyssid mites, "gynogenetic arrhenotoky" or "gynogenetic haplo-diploidy" is used to refer to parthenogenetic development of the eggs initiated by pseudogamy but the situation is different in phytoseiid mites where haplo-diploidy results in the production of biparental males which later in embryogenesis become haploid after losing the paternal set of chromosomes (Helle *et al.*, 1978; Hoy, 1979). The terms "parahaploidy" (Hartl and Brown, 1970) and "pseudo-arrhenotoky" (de Jong *et al.*, 1981), have been suggested for this unique phenomenon.

The Bryobinae are the most primitive sub-family within the Tetranychidae. In this group, haploidy results in females but as noted by Helle and Pijnacker (1985), "haploid thelytoky" and "diploid thelytoky" resulting from parthenogenesis is common. Distinction of the two is difficult in

thelytokous species with odd and even numbers of chromosomes. In the former, the offsprings are haploid while they are diploid in the latter as confirmed through egg squashes of the meiotic phase during embryogenesis (Pijnacker *et al.*, 1980).

Most Tetranychidae exhibit arrhenotoky whereby unfertilized females lay haploid eggs which give rise to haploid sons only and are therefore hemizygous. In the haploid system the sperms have an identical genotype like the males producing them and the latter can be regarded as "walking gametes" (Helle, 1965). Females are bisexual, originating from both parents (biparental), thus fertilized eggs give rise to diploid females only. The males are uniparental having inherited half the chromosomal complement (n=3) of their diploid mothers (2n=6). In such cases all genes act like dominants and there is no suppression of deleterious recessive alleles by normal dominants (Bruickner, 1975). In other words both dominant and recessive alleles are expressed in the partheno-produced haploid males (Helle, 1985).

The mechanism of sex determination in ticks is well reviewed (Sokolov, 1954; Goroshchenko, 1962; Kahn, 1964; Oliver, 1967). In

all the above cases all the offsprings are haploid (Helle and Pijnacker, 1985). It is for this reason that lethality is always expressed through the male haploidy as deleterious genes do not accumulate in a haplo-diploid system (Crozier, 1970). Under the same token, beneficial genes spreads rapidly under the same system. Unlike in the diploid systems, deleterious alleles and heterosis is only expressed in the diploid females. The variability common in diploid system due to overdominance is reduced by the male haploidy (Hartl, 1971). Inbreeding breaks down heterosis in diploid systems but haplo-diploid systems are less affected by inbreeding depression as the haploid part of the system is hemizygous (Helle, 1965, 1968; Eyndhoven and Helle, 1966)

The genetic basis behind this mode of sex determination is not well understood. In hymenopteran bees, maleness determining factors (M) are extra-chromosomal but female ones (F) are chromosomal, the interaction of MF + MFF determines sex (Goldschidt, 1934). In spider mites, a similar mechanism operates which in addition causes incompatiblity when M&F factors interact (Helle and Overmeer, 1973). Sex ratios are important in cross-breeding experiments because they indicate the proportion of the eggs

fertilized and therefore the level of compatibility between the hybridized populations. A relationship exists between the time spent in copulation and the sex-ratio (Boudreaux, 1963). This implies that apart from the rejection of a mating partner conspecificity is related to the length of time spent in copulation (Helle, 1967).

In arrhenotokous spider mite species females outnumber males (Helle and Pijnacker, 1985) giving a sex-ratio which may vary between 2:1 and 3:1 (Helle and Overmeer, 1973), 6:1 (Overmeer and Harrison, 1969) and to as high as 9:1 (Wrensch and Young, 1978). Helle, (1967) and later Helle and Overmeer (1973), stated that the sex-ratio is determined by the amount of sperm introduced during copulation. Genetically, the female determines which eggs are to be fertilized and therefore the sex-ratio (Mitchell, 1972). The sex-ratio in a particular strain of *T. urticae* remained fairly constant over several generations (Davis, 1952; Overmeer, 1967; Overmeer and Harrison, 1967) and *P. ulmi* (Putman, 1970; Cranham, 1973; Helle and Overmeer, 1973). It has been questioned why the spider mites should adopt a 3:1 ratio (Wrensch and Flechtmann, 1979). There is no *apriori* reason why this should be so unless the population has undergone an episode of very

low density whereby the probability of a male encoutering a quiescent teleiochrysalid is low resulting mainly in the production of haploid eggs and therefore a low sex ratio (Potter, 1977). The functional sex ratio determines the number of capable males and available females which under high densities, becomes high as more females are fertilized as frequency of encounter between sexes is higher giving a high sex ratio (Potter et al., 1976; Wrensch and Flechtmann, 1979). But earlier in the colonizing phase, females outnumber males as the males are competing for a small portion of the available females (Potter, 1977). Such information pertaining to *Mononychellus* is lacking.

2.6 Setae inheritance

Partial hybrid sterility among spider mites is attributed to intra-specific rather than inter-specific differerences (Gutierrez, 1987). This is borne out by the observed morphological variations in the setae patterns (Rogo *et al.*, 1987). It is conceivable that inter- and intra-continental introgression over the years of CGM populations via infested cassava germplasm (Belloti and Schoonhoven, 1978), has availed

populations with a divergent genetic make-up further contributing to this heterogeneity (Murega, 1989). Introgressive hybrids between allopatric populations can also give rise to heterogeneous intermediate populations (Balashov, 1979). Partial sterility can also arise as a result of the holocentric nature of spider mite's chromosomes resulting in many chromosome races (Helle, 1968) or from extra-chromosomal factors in the cytoplasm (de Boer, 1985). Heterogeneity detected in CGM populations from East Africa has been attributed to the occurrence of three setal types as exhibited by three mophologically distinguishable phenotypes.

Crosses made between red *T. telarius* x green coloured *T. urticae*, the resultant F_1 hybrids gave males only, but the backcross of F_1 hybrid sons x *T. urticae* females gave diploid females (Hussey and Parr, 1958). In addition, the crosses segregated into green (similar to F_1 hybrids), reddish and intermediate (changing from carmine to red). From this data, they concluded that body colour is controlled by a pair of non-allelic genes. However, Monroe (1963) argued that other factors such as the cytoplasm may be playing a role in colouration. Furthermore, as observed as early as 1913 by Ewing, chlorophyl plays part in colouration.

3.0 STUDY SITE SELECTION AND ECO-CLIMATIC ZONES

3.1 Site selection

Samples of CGM were collected from 19 sites in Kenya (Fig. 1). These sites were chosen from among five eco-climatic zones where cassava growing is important. The seasonal rainfall distribution among these zones is shown in Fig., 2. Collection of the samples was carried out during the dry season when CGM infestation is highest (Yaninek, 1984). In Kenya, this dry period occurs during the months of January-February. The CGM collection was based on its distribution in the five eco-climatic zones which differ with respect to their geographical location and the distance from each other.

3.2 Eco-climatic zones

3.2.1 The Coastal eco-zone (0-200 m)

This eco-climatic zone covers the districts of Kilifi, Kwale and Mombasa. It was felt necessary to compare the performance of hybrid offsprings derived from crosses between

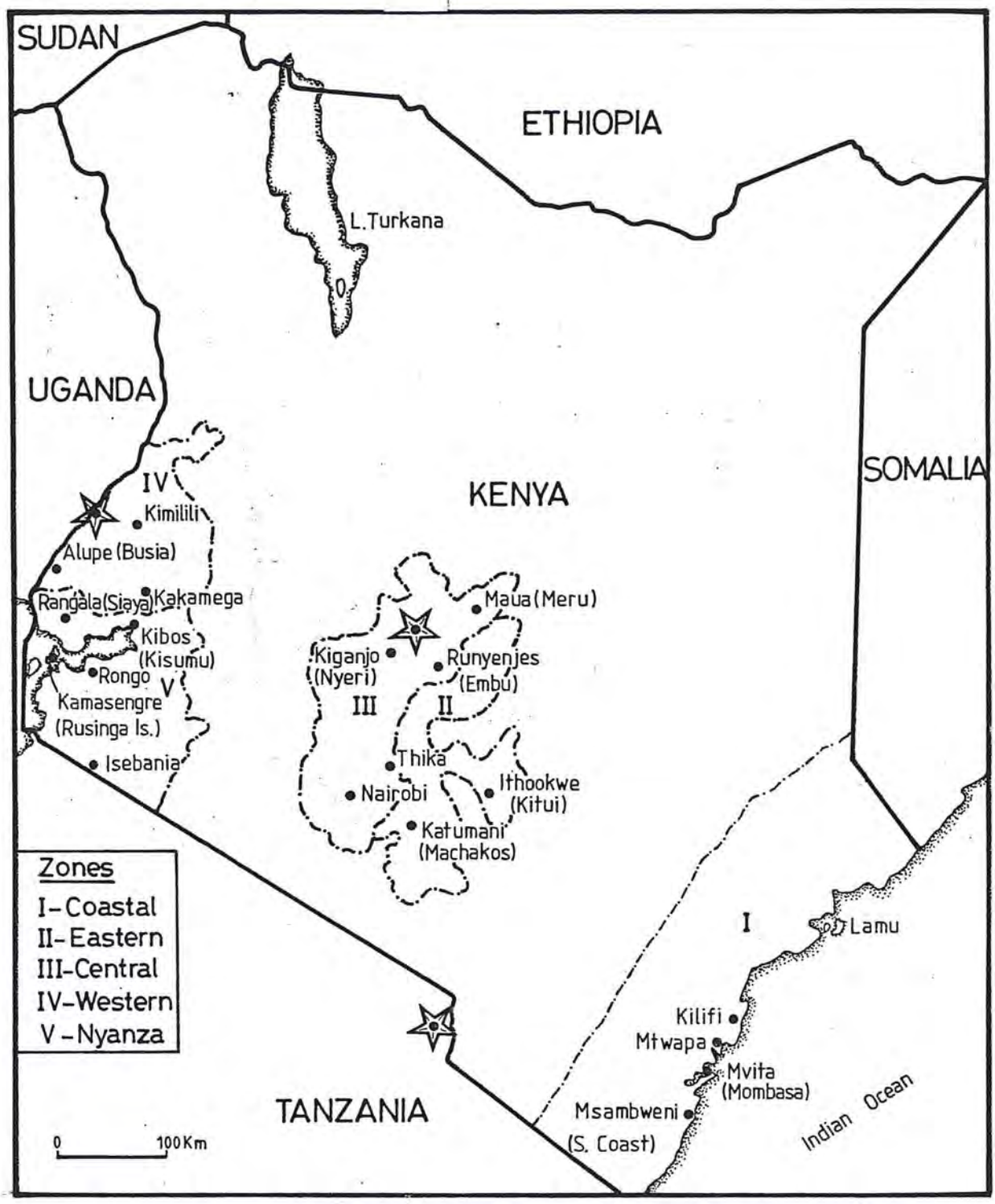

Fig. 1. Eco-climatic zones showing where cassava green spider mites (CGM) were sampled from

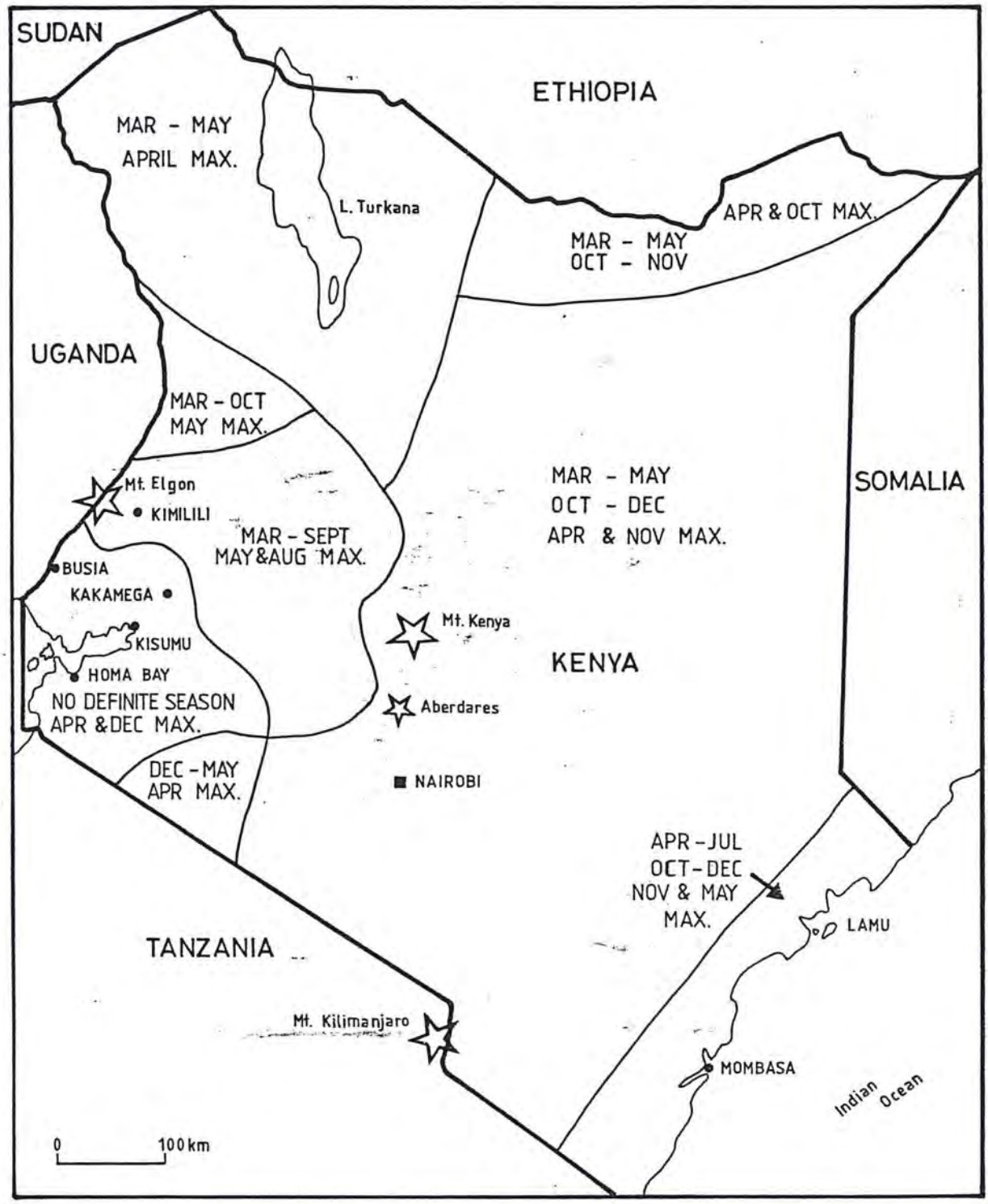

Fig. 2. Seasonal rainfall distribution among the five eco-climatic zones from which cassava green spider mites were sampled from

upcountry populations and those found at sea level. For this reason, CGM populations were collected from Msambweni (South Coast), Mvita (Mombasa island), Mtwapa and Kilifi (both in the North Coast). The coastal eco-zone is characterized by high humidity varying between 65-92% with an annual average value of 70% which is moderated by the coastal trade winds. High annnual temperatures and rainfall ranging from 26-30°C and 760-1270 mm respectively have been recorded. The total precipitation occurs mainly in one long spell between April-July with the peak in May. The October-December rains with the maximum in November are light and fall in the mornings as a result of cumulus clouds caused by morning trade winds. The months of January-March are dry. Such a climate is suitable for the cultivation of cassava which is the most important staple food among the coastal tribes. Other crops include sisal, maize, pulses, simsim, bixa, coconuts, and cashewnuts.

3.2.2 The Eastern eco-zone (1000-1500 m)

Certain areas in this zone which covers the districts of Machakos and Kitui may attain elevations of between 1500-2500 m above sea level. This is a semi-arid zone sandwiched between the

arid zone and the highlands east of the Rift valley. Annual rainfall is low and unreliable (500-750 mm, but can reach 1015 mm at higher elevations). Rainfall is unevenly distributed and occurs in two peaks, the long (March-May) and the short (October-December) rains. Maximum precipitation is in the months of April and November. Humidity ranges 40-70 % depending on the time of the year. The area is characterized by high temperatures (26-30°C.), so that evaporation rate is high. Temperatures may however fall to 22-26°C at higher elevations. In most cases there is a moisture deficit. This eco-zone is, therefore, a marginal farming area where crop failure is common leading to famine. The major subsistence crops are cassava, pulses, sorghum, and millets. Ranching is an important occupation among the Kamba inhabiting this region. Cassava is valued in this region not only because it is drought tolerant but also because it is the only reliable crop which can be harvested every 12-18 months during drought. The tubers needed for immediate consumption can be removed and others left in the soil to be harvested later. In addition the leaves can be eaten as a curry or fed to livestock when the grass is scarce.

3.3.3 The Central eco-zone (1500-3000 m)

This zone, referred to as the highlands east of the Rift Valley includes Nairobi and covers the districts of Kiambu, Muran'ga, Nyeri, Kirinyaga, Embu, Meru and Nyandarua. Mount Kenya (5182 m), the second highest mountain in Africa,the aberdares (3962 m), the Nyambene hills (1829 m) are heavily forested and exert a modifying influence on the climate in the areas surrounding them. The mean annual precipitation averages 760 mm in areas bordering the semi-arid region and rises to 1780 mm at higher elevations. As in the Eastern zone, rainfall is bimodal with the maximum precipitation occuring in April and November. Temperatures range from 22-26°C and could fall to as low as 8°C at higher elevations (range 8-15°C) during the cooler months of June-August. Humidity varies from 50-85% depending on the time of the year. This zone is a high potential farming area where coffee, tea, horticulture and dairying are the most important farming activities. Subsistence crops include cassava, maize, beans, vegetables and potatoes. The cultivation of cassava is not important and occurs sparsely.

3:3:4 The Western eco-zone (1500-2500 m)

This zone covers western province which includes the area around mount Elgon (4268 m) on the Kenya-Uganda border. The districts forming this region are Kakamega, Bungoma and Busia. This zone receives the highest rainfall among the other four which range from 760-1780 mm. The highest peak occurs from May-August. Temperatures range from 26-30°C. and relative humidity values similar to those of the lake zone depending on the elevation. Coffee, tea, maize, sugar cane, beans, millets and sorghum are grown. Cassava is particularly important in Bungoma and Busia districts where it is extensively grown.

3.3.5 The Nyanza eco-zone (1000-1500 m)

This is the area bordering the shores of lake Victoria covering the districts of Siaya, Kisumu, Kisii and South Nyanza. It is bordered by the western zone and the highlands west of the Rift Valley. Except for the leeward areas of South Nyanza, there is really no dry season in this area. Convectional rainfall being accompanied by thunder due to the influence of lake Victoria ranges 760-1525 mm annually. The highest rainfall

occurs during the months of April and December and is lowest during January-February. However, temperatures are very high ranging from 30-34°C, so that in most areas there is moisture deficit. Humidity is also high varying from 50-90% but averages of 60% have been recorded depending on the elevation and the time of the year. Sugar cane, sorghum, cassava and pulses are important farm crops in this region. Cassava is cut into chips, dried and then mixed with maize and sorghum and then ground into flour to make "ugali", a popular dish in this region.

4.0 GENERAL MATERIALS AND METHODS

4.1 Sampling proceedure

From the selected sites in each of the five eco-climatic zones, CGM samples were taken from leaf one to leaf five of the cassava plant where infestation is normally heaviest. Leaf 1 was regarded as the first fully expanded leaf from the shoot tip of the cassava plant. The infested leaves were placed in polythene bags (size 32x15 cm) and labelled with a water-proof Snowman^{R} G-T chisel tip marker pen according to the site sampled. To avoid the possibility of contamination, the samples were placed in individually labelled plastic lunch boxes (size 16x10x6 cm). Their lids were quickly replaced to avoid desiccation and the samples transported to the laboratory. In this way, samples could remain in good condition for a week. This proved useful when samples were to be taken from places distant from Mbita such as the coast.

4.2 Breeding protocol

In the laboratory, pure-bred lines for each of the 19 sites were established by pairing a

single virgin female (teleochrysalid) and a partheno-produced male from the same cassava leaf originating from the same locality. Unfertilized females lay eggs which give rise to males only. For this reason, the partheno-produced males were obtained from haploid eggs laid by 10 virgin females selected and reared separatetly from each of the 19 sites. The individual transfer of each mite on cassava leaf discs was achieved using a fine camel hair brush (size 00) under an M5 Wild Leitz stereo-microscope, at a magnification of x25. The cassava leaf discs were prepared using a cork borer (diameter ca.1.8 cm) from the 8th leaf of the susceptible cassava variety locally known as "Kibandameno" and which is grown at Mbita Point Field Station. The first-fifth fully expanded leaves are preferred by the mites. However, the eighth one was chosen because it is turgid enough to last from oviposition to eclosion of the mites' eggs before it deteroriates. The leaf discs were placed upperside down on water soaked cotton wool in perforated plastic Petri dishes (Petri-dish diameter ca.8.5 cm) The perforations in the plastic Petri dishes allow water from the holding plastic trays to pass into the cotton wool by capillary action keeping the leaf discs fresh (Plate 1), for at least 12 days when all the

Plate 1. Plastic Petri-dishes showing perforations through which water passes by capillary action

viable eggs were supposed to have hatched. In one generation, therefore, the leaf discs were replenished twice. Before the transfer of the mites was effected, the new leaf discs were checked under the microscope for presence of alien mites, predators or their eggs and if found, they were killed by puncturing them with a sharp pin. The Petri dishes containing the various CGM populations were placed in water-holding plastic trays (size 30x20x4 cm) (Plate 2). In addition, the wet cotton wool and the water in the holding trays act as barriers ensuring that mites remained in their respective leaf discs, thus avoiding contamination. This methodology is similar to the one originally used by Helle (1962) for spider mites of the *Tetranychus urticae* group, but was modified to suit studies on *Mononychellus* by Murega (1989).

4.3 Colony propagation

The eggs obtained from the male and female pair from each of the 19 sites were separately allowed to hatch and mature into adults. These experiments were carried out under normal room conditions where temperature and relative humidity varied from 27±3°C. and 75±15 %

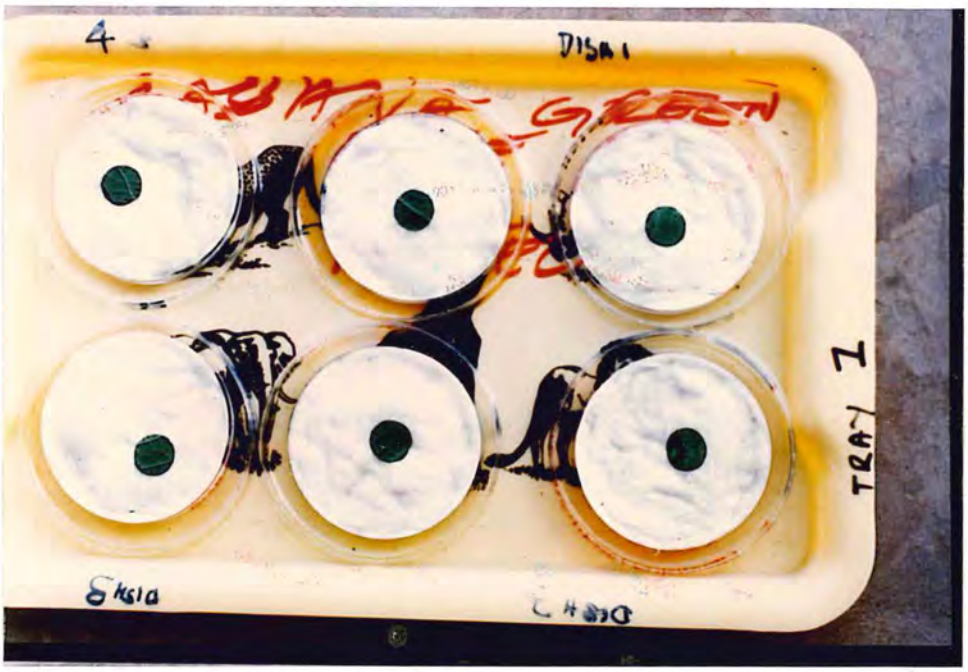

Plate 2. Plastic trays used for holding Petri-dishes containing CGM populations reared on cassava leaf discs

r.h. The holding plastic trays containing all the desired crosses on leaf discs placed in separate plastic Petri-dishes were placed inside an improvised growth chamber (size, 105x60x60 cm) made of mite-proof cloth which was in turn placed inside a galvanized metal trough containing water (size, 90x90x15 cm). In addition, a 100 W incandescent bulb was used to illuminate the chamber and to provide the necessary warmth. Inside this chamber (Plate 3), the conditions remained relatively stable at 29±1°C.and 80±5 r.h. The mite-proof cloth and the water inside the trough kept off flying insects and other contaminants.

By the 15th day, the CGM populations are already in their early adult life. It is at this stage that the adult CGM samples were divided into 2, one lot being kept in the laboratory as a back-up colony while the other one was infested on individually caged potted cassava plants (of the susceptible variety locally known as "Kibandameno").

Over a period of time and because of their short mean generation times, laboratory reared CGM populations may lose heterosis. This is because in haplo-diploid organisms inbreeding depression manifested by deleterious alleles and

Plate 3. Improvised growth chamber in which CGM populations were incubated

breakdown of heterosis may occur as a result of sib-mating (Eyndhoven and Helle, 1966). This may lead the laboratory maintained cultures to differ from the wild type. It is for this reason that CGM populations representing each of the 19 sites were propagated on potted cassava plants in the screen house. The population size representing each of the 19 sites never dropped below an estimated 1,000 individuals per potted cassava plant. This enabled populations to have a wider genetic base from the expanded population in which random mating occurred (cf. Helle, 1968).

To infest the CGM on the potted cassava plants, cassava leaf discs containing 10 males and 10 females reared separately and in isolation from each of the 19 sites were pinned on the leaves of the potted cassava plants. As the leaf discs withered, the mites automatically transferred themselves by walking to the fresh leaves of the potted cassava plants.

To avoid contamination between the strains themselves and/or any exogeneous contaminants, the potted cassava plants were kept isolated from one another. This was accomplished by placing the potted cassava plants in cages made of mite-proof cloth (size 105x60x60 cm), the cages were positioned 3 m apart inside the screen house

(measuring 11x7.5 m) (Plate, 4). In addition, the cages were placed in shallow galvanized water-holding metal troughs (size 90x90x15 cm) (Plate, 5), to further isolate them from any contamination.

4.4 Hybridization and genetic isolation studies

Samples of CGM were collected from the caged plants representing the 19 geographical populations one month after being artificially infested and brought to the laboratory for hybridization and reproductive isolation studies.

4.4.1 Inter-populational compatibility experiments

Inter-population hybridization was carried out by pairing 10 virgin females (teleiochrysalids) and 10 partheno-produced virgin males from any two of the desired 19 localities on cassava leaf discs placed in Petri-dishes. The mites were allowed to oviposit for 48 hours. The parents were then removed and the F_1 eggs deposited were counted. Hatching of the eggs usually occurred after 6 days and the number of

Plate 4. Screen house in which CGM populations were reared and isolated

Plate 5. Mite-proof cages in which CGM populations were isolated

unhatched eggs in all crosses were scored at day 10, when unhatched eggs were considered either non-viable or dead.

The F_2 generation was obtained from 10 sib-mated F_1 females at day 15. These were Tisolated on fresh leaf discs and the number of non-viable eggs scored 10 days later. The F_3 generation similarly was obtained from 10 F_2 females fertilized in the same way. Reciprocal crosses were carried out in a similar manner and egg lathality scored.

4.4.2 Intra-populational compatibility experiments

The intra-population crosses were performed in both directions in order to check the heterogeneity or homogeneity of the populations This was done for all the 19 populations over 3 filial generations (G_1 , G_2 , and G_3). Ten mated females, of each population were placed on rearing leaf discs and G_1 generation eggs obtained. Mortality was scored 10 days later. Viable offspring was reared to adulthood and 10 sib-mated females were further isolated for rearing of the G_2 siblings. Similarly, 10 females were used to produce G_3 generation.

4.5 Sex inheritance and sex-ratio studies

To verify whether *Mononychellus* exhibit arrhenotoky like other members of the Tetranychidae, 10 virgin females from each of the 19 geographical populations were isolated on cassava leaf discs and allowed to oviposit for 48 hours. The offspring were allowed to mature and the resultant siblings sexed 15 days later.

The sex ratio in Tetranychid spider mites is always in favour of females such that a ratio of 3:1 is regarded as "normal" (Helle and Overmeer, 1973). However ratios of 6:1 Overmeer and Harrison, 1969) and 9:1 (Wrensch and Young, 1978) have been reported. To test whether the progeny of the 19 populations conform to the established sex ratios, an equal number of virgin males and females were paired for each population. In this way, competition for mates was reduced as each male ideally had its own partner. Secondary sibling sex ratios were then scored.

4.6 Genetic stability of dorso-central hysterosomal setae

The understanding of the mechanism of the genetic inheritance of the setae is important since these are the parameters used by morphologists to designate CGM species. There have been questions as to whether these are stable or reliable species diagnostic characters (Gutierrez, 1987; Rogo et *al.*, 1987). For this reason, 6 sites were selected from the 19 from which the mechanism of setae inheritance were studied.

From each of the 6 sites, a virgin male and female were paired for a period of 24 hours. The males were then removed and preserved in 70% alcohol for mounting later. The females were allowed to oviposit for 48 hours before similarly being preserved.

The eggs laid were recorded and allowed to hatch and the subsequent F_1 generation allowed to mature to adulthood. The setae lengths, their distances from each other as well as the total body lengths of the founder parents and the F_1 generation were measured and correlations between these parameters examined. These observations were important in ascertaining whether the observed partial sterility in the hybridization experiments

could be linked to the heterogeneity of the setae patterns.

4.6.1 Mounting

The alcohol preserved specimens were mounted in a laboratory prepared Hoyer's medium. Hoyer's medium consists of distilled water (40 mls), gum arabic crystals (30 g), chloral hydrate (200 g) and glycerine (20 g) These components were mixed in the laboratory at room temperature in the sequence listed, stirring the contents over a period of 7 days before the medium was ready for use (cf. Gutierrez, 1985).

During the mounting, the specimens were placed in the centre of the mountant on a clean slide (20x60 mm). The females were oriented dorsal side-up in order to reveal their hysterosomal setae while the males were mounted in profile i.e. laterally in order to facilitate the examination of the aedeagus. A round cover slip (diameter, 12 mm) was then placed carefully over the specimen and the slide warmed gently over a spirit lamp until bubbles appeared in the solution. The heating clears and expands the specimen. Any air bubbles trapped in the mountant migrated to the

periphery of the slide as the specimen relaxed and the appendages stretched outwards.

To further clear the specimen, the slides were placed in an oven set at 40°C. The slides were dry and ready for examination after 14 days. The Hoyer's medium is hygroscopic and unstable in humid conditions (Gutierrez, 1985). For this reason, the dry slides were then sealed by ringing with Euparal in order to obtain a permanent slide preparation.

4.6.2 Measurements of the hysterosomal setae and examination of the aedegii

The females' hysterosomal setae (the D_1, D_2 & D_3) (Plate 6), were measured using an M29 Wild Leitz phase contrast microscope and classified (cf. Rogo *et al.*, 1987). Before measurements were taken, calibration of the microscope was carried out by overlapping the eye piece graticule readings onto the stage micrometer. The length of the individual setae D_1, D_2 and D_3 as well as their respective longitudinal distances taken from their bases, D_1-D_2 (distance 1) and D_2-D_3 (distance 2) were measured under x40 magnification while the total body length was

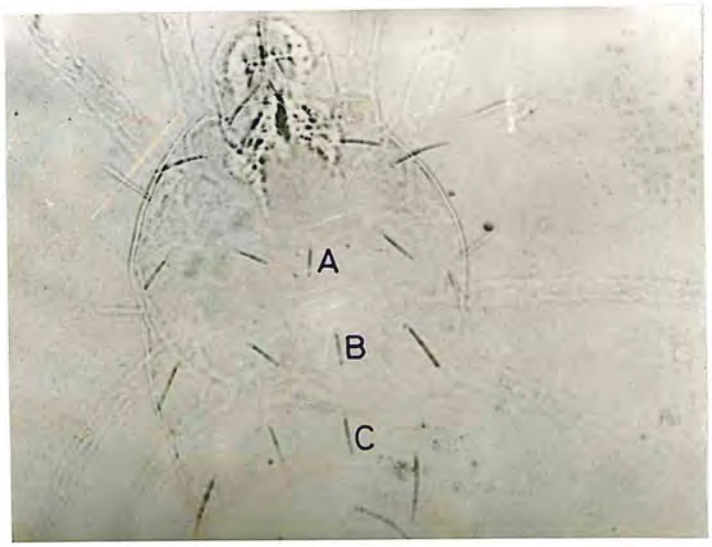

Plate 6. Dorso-central hysterosomal setae (D_1, D_2 and D_3) of a typical CGM female (a=D_1, b=D_2 and c=D_3 setae respectively, X1000 times)

measured from the tip of the infracapitulum to the distal anal tip under the x10 magnification (Fig. 24). The mean length of the hysterosomal setae was calculated using the following formula $(D_1+D_2+D_3)/3$. All the measurements were read in millimicrons (µm).

The eye piece graticule divisions recorded for each individual measurements were converted to millimicron readings by multiplying the respective values of every variable reading by a weighting coefficient equivalent to a single division in the objective. For x10 and the x40 objective the weighting coefficients were x2.86 and x11.76 respectively. The setae lengths recorded were then categorized using the method developed by Rogo *et al.*, (1987), (Table, 1).

Tetranychid spider mites males are haploid. During copulation, the male's aedeagus and the female's vagina are a critical lock-and-key system (Gutierrez, 1985). This is a species-specific system which ensures that only members of the same species can mate. The determination of the species of the male is, therefore, important in taxonomy of freely interbreeding individuals.

For the above reason, the shapes of the aedeagii of 10 representative males from each of the 19 sites were examined under oil emersion lens

Table 1: Dorso-central hysterosomal setae classification of CGM specimens (divisions of the eye piece graticule, after Rogo et al., (1987)

D_1	D_2	D_3	
≤ 7	≤ 9	≤ 11	Short setae
≥ 10	≥ 11	≥ 15	Long setae

Values between the long and the short categories were classified as intermediate.

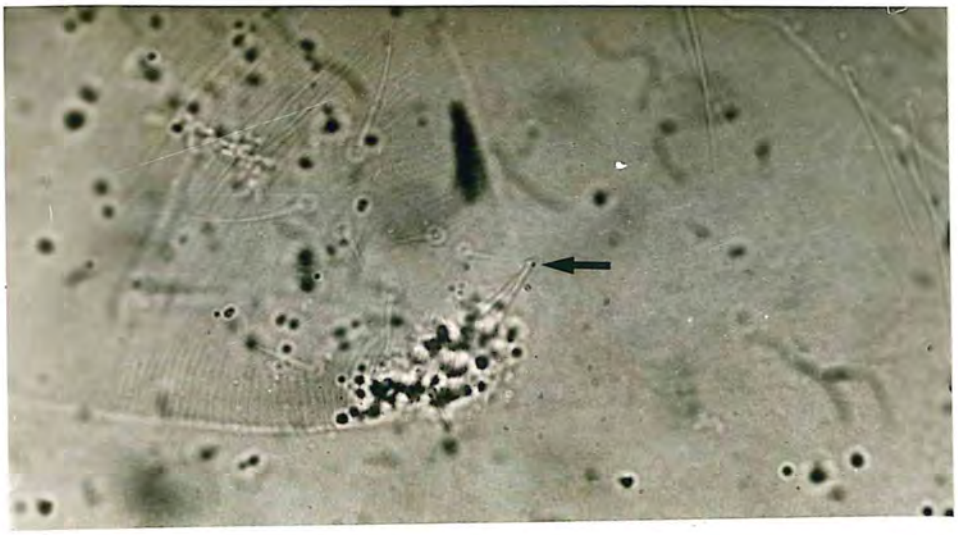

Plate 7. The male terminalium of M. progresivus, detected in the populations handled (arrow, X1000 times)

of an M29 Wild Leitz phase contrast microscope. The aedeagii seen in all the specimens were carefully photographed (Plate, 7).

4:7 Data analysis

Finally, the egg mortality data for both inter- and intra-population hybridization crosses were subjected to statistical analysis using the two way analysis of variance (Steel and Torrie, 1960; Gomez and Gomez, 1984). Differences among the F_1, F_2 and F_3 as well as between the G_1, G_2, and G_3 filial progenies and their respective reciprocal crosses were assessed.

For the setae inheritance studies the analysis was performed using a SAS (Statistical Analysis System) statistical software package. Correlation between the lengths of these setae (D_1, D_2 and D_3), their longitudinal distances (distances 1 and 2) and the total body length was examined. Correlation was also examined between the mean setae length and the longitudinal distances between the hysterosomal setae and the body length. Relationship of the ratio of the setae length and their inter-setal distances to the body length was also examined.

5.0 INTER-POPULATIONAL COMPATIBILITY CROSSES

5.1 Introduction.

The two CGM species reported from Africa have been distinguished on the length of their dorso-central hysterosomal setae (D_1, D_2 and D_3) in relation to their distances apart (D_1-D_2 and D_2-D_3) on the female dorsum (Flechtmann and Baker, 1970; Flechtmann, 1981; Doreste, 1982). Prior to the work of Doreste (1982), the males were not utilized for species diagnosis although Ewing (1913), had pointed out the significance of the profile of the male terminalium for this purpose. Due to the unreliability of the morphological criteria to identify the species some taxonomists using other diagnostic methods have concluded that probably only one species occurs (Gutierrez, 1987; Nokoe and Rogo, 1988).

The level of conspecificity between 19 CGM populations from Kenya were used to establish the magnitude of inter-populational compatibility among the test populations by hybridization. Hybridization was used to confirm whether free gene exchange occurs among the test populations. This technique has been used to resolve taxonomic

problems among spider mites notably, the *Tetranychus urticae* group (Boudreaux, 1963; Helle and Pieterse, 1965; Overmeer and van Zon, 1976), *T. cinnabarinus* (Monroe, 1963; Jordaan, 1977), *T. neocalodenicus* complex (Gutierrez and van Zon, 1976). In the present studies 122 crosses in all directions including reciprocal crosses were carried out and the percentage of egg lethality assessed.

5.2 Materials and Methods.

Samples of CGM were collected from Msambweni (South Coast), Mvita (Mombasa island), Mtwapa, Kilifi (North Coast), Katumani (Machakos), Ithookwe (Kitui), Nairobi, Thika, Runyenje's (Embu), Maua (Meru), Kiganjo (Nyeri), Alupe (Busia), Kimilili, Kakamega, Rang'ala (Siaya), Kibos (Kisumu), Rongo, Kamasengre (Rusinga island) and Isebania (Fig. 1). The mites came from the various eco-climatic zones (Fig. 2) and were then transferred to the laboratory where hybridization and reproductive isolation studies were carried out. The hybridization tests were done among CGM populations from:

1. Coastal CGM populations
2. Coastal and upcountry (Ithookwe (Kitui), Maua

(Meru), Isebania and Alupe (Busia) populations

3. Eastern CGM populations

4. Central CGM populations

5. Nyanza and Western CGM populations

Unfertilized females exhibit arrhenotoky. For this reason unmated virgin males can be obtained which are not deficient in sperms (Helle 1967; Jordaan, 1977). Such males were obtained in the present studies by placing 10 virgin females (teleiochrysalids) on cassava leaf discs and allowing them to oviposit. In 14 days the eggs had hatched and mature virgin males obtained.

Inter-strain hybridization was carried out by pairing 10 teleiochrysalids and 10 unmated males from any of the desired localities. The proceedure followed is as outlined in 4.4.1. Hatching of the eggs occur after 6 days and unhatched eggs in all crosses was scored at day 10.

The F_2 generation was obtained from 10 fertilized F_1 females isolated on fresh leaf discs at day 15 and the number of non-viable eggs scored 10 days later. The F_3 generation was obtained from 10 fertilized F_2 females in a similar manner. The lethality recorded is calculated from 4 "egg waves" which represents fecundity of 10 females.

5.3 Results

Hybridization data among the 19 populations are shown in Tables, 2-9 and Figs., 3-17). Among all the populations hybridized partial incompatibility was demonstrated (Tables, 2-9). Lethality of eggs of varying magnitude was observed in the F_1, F_2 and F_3 generations (Table 2-9). Mean eggs lethality was highest in the F_2. The highest mean value were obtained from the eco-climatic zones of Nyanza and Western Kenya. Values of 11.43 and 11.69% in a test cross and a reciprocal cross between Rusinga x Busia and Siaya x Kakamega respectively were obtained. Mortality was significantly lower in the the F_3 and F_1 in that order when compared to the F_2 ($p< 0.0003$; Appendices, 1 and 2; Tables, 2 and 3; Figs., 3 and 4). From among the five eco-climatic zones, overall partial hybrid sterility was highest among the Nyanza and Western Kenya as well as the Coastal and up-country CGM populations compared to the Eastern and Central Kenya CGM populations. The F_2 lethality varied from 11.43, 9.26 and 6.35% respectively (Tables, 2-9; Figs., 3-9).

The trend which can be discerned is that group mortality means for crosses and their reciprocals are lowest in the F_3 than F_1 and

Table 2. Inter-populational hybrid crosses in three filial generations (F_1, F_2 and F_3) of some CGM populations collected from eco-climatic zones of Nyanza and Western, Kenya.

Collection Site	% Egg lethality (No. of eggs laid in brackets)			Sex-ratio (Female:male)		
	F_1	F_2	F_3	F_1	F_2	F_3
Rusinga X Rongo	4.16(192)	7.76(464)	0.00(155)	3:1	3:1	5:1
Rusinga X Kibos	6.59(182)	11.14(359)	0.48(207)	2:1	3:1	5:1
Rusinga X Kakamega	4.45(132)	10.68(309)	0.37(268)	3:1	2:1	4:1
Rusinga X Siaya	6.25(112)	6.55(336)	0.63(160)	4:1	3:1	5:1
Rusinga X Busia	9.73(185)	11.43(175)	0.53(190)	4:1	3:1	5:1
Rongo X Kibos	4.32(139)	8.29(398)	5.15(272)	2:1	3:1	5:1
Rongo X Siaya	0.00(170)	3.61(305)	0.00(379)	5:1	2:1	3:1
Rongo X Kakamega	4.00(100)	7.47(241)	0.38(261)	3:1	3:1	3:1
Rongo X Siaya	0.00(170)	3.61(305)	0.00(379)	5:1	2:1	3:1
Rongo X Busia	0.86(233)	1.42(211)	0.00(192)	4:1	5:1	2:1
Kibos X Siaya	3.36(268)	3.30(303)	1.76(340)	6:1	2:1	2:1
Kibos X Kakamega	8.85(113)	10.57(388)	1.08(186)	4:1	3:1	4:1
Kibos X Busia	5.38(130)	7.57(304)	0.00(180)	3:1	2:1	2:1
Kakamega X Siaya	1.18(169)	1.35(297)	0.81(248)	5:1	2:1	3:1
Kakamega X Busia	1.15(260)	2.56(273)	0.78(256)	5:1	3:1	2:1
Siaya X Busia	6.79(103)	7.14(280)	2.80(214)	3:1	3:1	3:1

Table 3. Reciprocal crosses in three filial generations (F_1, F_2 and F_3) of some CGM populations collected from eco-climatic zones of Nyanza and Western, Kenya.

Reciprocal cross	% Egg lethality (No. of eggs laid in brackets)			Sex-ratio (Female:male)		
	F_1	F_2	F_3	F_1	F_2	F_3
Rongo x Rusinga	6.60(106)	7.56(344)	0.00(243)	2:1	2:1	5:1
Kibos x Rusinga	1.39(286)	1.43(279)	1.01(199)	5:1	5:1	2:1
Kakamega x Rusinga	2.32(259)	2.19(273)	0.59(335)	6:1	3:1	2:1
Siaya x Rusinga	9.41(85)	6.64(256)	0.43(230)	2:1	3:1	6:1
Busia x Rusinga	5.76(191)	7.43(259)	4.12(170)	4:1	2:1	4:1
Kibos x Rongo	3.41(88)	11.31(336)	5.38(223)	3:1	3:1	5:1
Kakamega x Rongo	0.00(337)	2.48(202)	1.68(357)	5:1	2:1	3:1
Siaya x Rongo	4.50(111)	8.02(212)	0.41(247)	5:1	3:1	4:1
Busia x Rongo	3.47(173)	9.84(376)	4.12(170)	4:1	2:1	4:1
Kakamega x Kibos	3.39(182)	4.17(552)	0.72(139)	3:1	5:1	4:1
Siaya x Kibos	9.30(86)	6.97(201)	3.28(183))	4:1	2:1	2:1
Busia x Kibos	1.96(407)	4.37(412)	3.96(328)	6:1	3:1	2:1
Siaya x Kakamega	5.88(58)	11.69(265)	0.94(212)	3:1	3:1	3:1
Busia x Kakamega	4.50(94)	10.18(296)	2.69(186)	4:1	3:1	5:1
Busia x Siaya	5.49(225)	3.50(257)	3.11(257)	4:1	2:1	2:1

Table 4. Inter-populational hybrid crosses between some CGM populations collected from eco-climatic zones of Eastern, Central and Western Kenya.

Hybrid cross (Female x Male)	% Egg lethality (No.of eggslaid in brackets)			Sex-ratio (Female: Male)		
	F_1	F_2	F_3	F_1	F_2	F_3
Nairobi x Thika	1.13(441)	3.51(171)	1.09(273)	3:1	3:1	3:1
Nairobi x Embu	0.59(168)	6.27(255)	0.00(347)	2:1	2:1	2:1
Nairobi x Meru	2.08(240)	4.40(250)	0.59(508)	3:1	2:1	2:1
Nairobi x Nyeri	0.56(179)	1.39(286)	0.80(375)	1:1	2:1	2:1
Nairobi x Kitui	2.29(218)	4.69(149)	1.13(355)	3:1	2:1	3:1
Nairobi x Machakos	1.19(336)	2.46(203)	1.09(546)	3:1	3:1	3:1
Nairobi x Kimilili	2.66(301)	2.58(155)	0.64(622)	3:1	2:1	3:1
Thika x Embu	1.03(290)	2.54(197)	0.70(285)	2:1	3:1	3:1
Thika x Meru	0.61(190)	0.71(282)	0.00(194)	2:1	1:1	2:1
Thika x Nyeri	0.46(216)	2.63(152)	1.02(295)	3:1	2:1	2:1
Thika x Kitui	2.32(302)	3.21(218)	0.93(215)	2:1	2:1	2:1
Thika x Machakos	1.61(372)	3.05(197)	1.65(239)	5:1	3:1	4:1
Thika x Kimilili	0.78(128)	1.33(301)	1.39(288)	3:1	4:1	4:1
Embu x Meru	1.30(307)	1.97(152)	2.56(234)	3:1	3:1	3:1
Embu x Nyeri	0.84(475)	1.75(114)	0.72(279)	7:1	5:1	2:1
Embu x Kitui	2.09(286)	6.13(212)	1.87(214)	3:1	3:1	2:1
Embu x Machakos	2.02(248)	5.08(177)	0.76(396)	2:1	6:1	6:1
Embu x Kimilili	1.89(212)	1.93(207)	0.86(349)	4:1	3:1	5:1
Meru x Nyeri	1.44(209)	1.67(360)	0.46(219)	4:1	4:1	3:1
Meru x Kitui	2.09(287)	2.43(288)	0.64(314)	3:1	2:1	2:1
Meru x Machakos	2.02(445)	2.70(296)	0.82(244)	3:1	3:1	2:1
Meru x Kimilili	0.85(234)	2.58(155)	0.52(388)	3:1	6:1	5:1
Nyeri x Kitui	0.00(320)	3.74(187)	0.93(214)	8:1	5:1	3:1
Kitui x Machakos	0.53(189)	4.27(117)	0.94(319)	4:1	3:1	3:1
Kitui x Kimilili	1.79(339)	1.19(168)	0.89(223)	3:1	6:1	2:1
Nyeri x Machakos	1.04(193)	2.10(238)	0.96(313)	5:1	2:1	3:1
Machakos x Kimilili	1.91(157)	2.46(285)	0.00(234)	3:1	2:1	3:1
Nyeri x Kimilili	1.62(308)	3.60(222)	0.00(138)	2:1	6:1	3:1

Table 5. Reciprocal crosses between some CGM populations collected from eco-climatic zones of Eastern, Central and Western Kenya.

Reciprocal Cross (Female x Male)	% Egg lethality (No.of eggslaid in brackets)			Sex-ratio (Female: Male)		
	F1	F2	F3	F1	F2	F3
Thika x Nairobi	1.79(390)	2.97(236)	0.73(275)	2:1	3:1	3:1
Embu x Nairobi	2.16(324)	3.49(229)	0.78(128)	4:1	4:1	6:1
Meru x Nairobi	1.47(339)	2.07(242)	0.29(341)	3:1	2:1	3:1
Nyeri x Nairobi	0.88(227)	1.32(152)	0.74(403)	6:1	2:1	2:1
Kitui x Nairobi	2.94(272)	3.04(230)	0.00(213)	2:1	2:1	2:1
Machakos x Nairobi	0.87(231)	3.15(159)	0.40(247)	6:1	3:1	4:1
Kimilili x Nairobi	1.35(296)	4.48(134)	0.88(340)	3:1	3:1	3:1
Embu x Thika	3.14(159)	2.34(214)	0.00(398)	2:1	2:1	2:1
Meru x Thika	1.86(161)	2.63(114)	0.77(260)	2:1	3:1	3:1
Nyeri x Thika	0.55(180)	1.32(152)	1.59(377)	1:1	2:1	3:1
Kitui x Thika	2.74(328)	4.02(174)	0.00(268)	3:1	3:1	2:1
Machakos x Thika	1.41(142)	4.54(264)	0.87(343)	4:1	3:1	4:1
Thika x Kimilili	0.78(128)	1.33(301)	1.39(288)	3:1	4:1	4:1
Meru x Embu	0.00(287)	1.15(174)	0.93(216)	6:1	6:1	3:1
Nyeri x Embu	1.17(257)	1.83(328)	0.43(235)	6:1	3:1	4:1
Kitui x Embu	1.01(271)	1.56(193)	0.68(146)	3:1	8:1	4:1
Machakos x Embu	2.41(290)	6.35(126)	1.08(279)	5:1	4:1	4:1
Kimilili x Embu	3.08(130)	4.88(123)	1.44(347)	3:1	3:1	4:1
Nyeri x Meru	1.41(142)	2.32(302)	0.75(134)	6:1	4:1	3:1
Kitui x Meru	0.82(243)	2.06(194)	0.00(220)	2:1	2:1	2:1
Machakos x Meru	0.71(140)	2.14(280)	0.31(320)	3:1	3:1	4:1
Kimilili x Meru	3.39(206)	4.72(212)	0.93(430)	4:1	5:1	5:1
Kitui x Nyeri	0.55(361)	2.17(184)	0.45(224)	5:1	6:1	4:1
Machakos x Kitui	2.59(309)	2.82(177)	0.94(319)	3:1	3:1	3:1
Kimilili x Kitui	0.75(268)	1.42(352)	0.73(137)	3:1	3:1	5:1
Machakos x Nyeri	2.46(244)	3.33(180)	1.30(461)	4:1	3:1	5:1
Kimilili x Machakos	2.39(209)	3.97(126)	0.76(262)	3:1	3:1	3:1
Kimilili x Nyeri	1.68(417)	4.96(121)	0.76(264)	3:1	3:1	2:1

Table 6. Inter-populational hybrid crosses in three filial generations (F_1, F_2 and F_3) of some CGM populations collected from Coastal eco-climatic zone.

Hybrid cross	% Egg lethality (No. of eggs laid in brackets)			Sex-ratio (Female:male)		
	F_1	F_2	F_3	F_1	F_2	F_3
Msambweni x Mvita	3.27(144)	9.26(142)	1.01(296)	1:1	2:1	2:1
Msambweni x Mtwapa	3.67(222)	7.59(217)	0.61(300)	2:1	2:1	2:1
Msambweni x Kilifi	4.10(167)	7.31(211)	1.54(291)	2:1	1:1	2:1
Mvita x Kilifi	2.88(192)	6.28(271)	1.01(270)	2:1	2:1	2:1
Mvita x Mtwapa	3.28(208)	6.58(271)	0.97(327)	2:1	1:1	2:1
Mtwapa x Kilifi	5.57(176)	7.80(210)	1.09(313)	2:1	2:1	2:1

Table 7. Reciprocal crosses in three filial generations (F_1, F_2 and F_3) of some CGM populations collected from Coastal eco-climatic zone.

Reciprocal cross	% Egg lethality (No. of eggs laid in brackets)			Sex-ratio (Female:male)		
	F_1	F_2	F_3	F_1	F_2	F_3
Mvita x Msambweni	4.28(174)	6.88(237)	1.59(318)	3:1	2:1	2:1
Mtwapa x Msambweni	2.88(142)	8.18(165)	2.31(215)	3:1	2:1	2:1
Kilifi x Msambweni	3.67(205)	6.79(222)	1.15(319)	2:1	2:1	2:1
Kilifi x Mvita	4.54(141)	7.32(135)	1.97(384)	2:1	2:1	2:1
Mtwapa x Mvita	5.43(142)	8.10(232)	1.83(262)	2:1	1:1	2:1
Kilifi x Mtwapa	3.85(213)	7.76(155)	3.36(218)	2:1	2:1	2:1

Table 8. Inter-populational hybrid crosses in three filial generations (F_1, F_2 and F_3) of some CGM populations collected from Coastal and up-country eco-climatic zone.

Hybrid cross	% Egg lethality (No. of eggs laid in brackets)			Sex-ratio (Female:male)		
	F_1	F_2	F_3	F_1	F_2	F_3
Meru x Msambweni	4.47(188)	6.48(149)	0.90(174)	2:1	2:1	2:1
Meru x Kilifi	4.56(118)	6.67(205)	1.60(201)	1:1	2:1	2:1
Meru x Isebania	4.21(293)	8.79(139)	2.16(134)	3:1	2:1	2:1
Kitui x Msambweni	5.25(280)	6.99(140)	2.10(295)	2:1	2:1	2:1
Kitui x Isebania	3.64(327)	8.22(133)	1.57(154)	2:1	2:1	2:1
Isebania x Msambweni	5.85(199)	8.88(266)	1.14(112)	2:1	1:1	2:1
Isebania x Kilifi	3.57(184)	5.96(128)	2.23(301)	2:1	2:1	2:1
Isebania x Busia	3.64(278)	5.40(185)	1.71(217)	3:1	2:1	2:1
Busia x Msambweni	3.79(236)	6.20(127)	2.64(281)	4:1	2:1	2:1
Busia x Kilifi	3.29(137)	5.40(125)	1.28(165)	3:1	2:1	2:1
Kitui x Kilifi	5.27(178)	8.76(136)	3.73(266)	2:1	2:1	2:1

Table 9. Reciprocal crosses in three filial generations (F_1, F_2 and F_3) of some CGM populations collected from Coastal and up-country eco-climatic zone.

Reciprocal cross	% Egg lethality (No. of eggs laid in brackets)			Sex-ratio (Female:male)		
	F_1	F_2	F_3	F_1	F_2	F_3
Msambweni x Meru	4.77(238)	7.54(111)	1.03(120)	2:1	2:1	2:1
Msambweni x Kitui	4.20(271)	6.86(113)	2.21(194)	3:1	2:1	2:1
Msambweni x Isebania	5.10(240)	7.21(197)	2.69(1514)	1:1	3:1	2:1
Msambweni x Busia	3.40(163)	7.04(208)	1.86(305)	2:1	2:1	2:1
Kilifi x Kitui	3.17(257)	8.41(191)	0.99(211)	2:1	2:1	2:1
Kilifi x Meru	3.66(282)	7.36(232)	2.91(145)	2:1	2:1	2:1
Kilifi x Isebania	5.97(306)	6.80(144)	0.85(179)	2:1	2:1	2:1
Kilifi x Busia	4.37(183)	7.08(150)	2.36(307)	2:1	2:1	2:1
Isebania x Meru	4.81(183)	7.92(216)	2.22(245)	2:1	2:1	2:1
Isebania x Kitui	2.98(186)	5.84(121)	0.80(222)	2:1	2:1	2:1
Busia x Isebania	5.12(218)	8.67(166)	2.85(350)	2:1	2:1	2:1

highest in the F_2 ($F_1 < F_2 > F_3$) (Figs., 10-17; Appendices 1-8; $p<0.0003$). The student-Newman-Keuls test ranks the group filial generation mortality in the order just mentioned (Appendices 1-8). Highly significant differences occur between filial generations ($P<0.0001$) and "egg waves" (replications) ($P>0.0001$). Graphical representation of the egg lethality data is shown in Figs., 3-17 whereby total mortalities of approximately 10, 30 and 50%. for the F_3, F_1 and F_2 generations respectively, were calculated. In all the crosses and their reciprocals among CGM populations from the five eco-climatic zones, the trend in egg lethality is the same such that $F_1 < F_2 > F_3$. The mortality as expected is highest in the F_2 but dramatically drops in the F_3 to give a vigorous progeny $p<0.0001$; Appendices, 1-8). However, values of filial generations over the individual "egg waves" (interaction) was not significant among populations from Nyanza and Western Kenya and the coastal populations ($p>0.05$; appendices 1,2 and 5-8) whereas inter-populational hybrids from Central and Eastern Kenya were significantly different ($p<0.05$; Appendix, 3 and 4) suggesting that the populations from Central Kenya are genetically different. However, this observation is not supported by the data in Tables

F_1= First filial generation

F_2= Second filial generation

F_3= Third filial generation

Legend for Fig., 3

1. Rusinga X Rongo
2. Rusinga X Kibos
3. Rusinga X Kakamega
4. Rusinga X Siaya
5. Rusinga X Busia
6. Rongo X Kibos
7. Rongo X Siaya
8. Rongo X Kakamega
9. Rongo X Siaya
10. Rongo X Busia
11. Kibos X Siaya
12. Kibos X Kakamega
13. Kibos X Busia
14. Kakamega X Siaya
15. Kakamega X Busia
16. Siaya X Busia

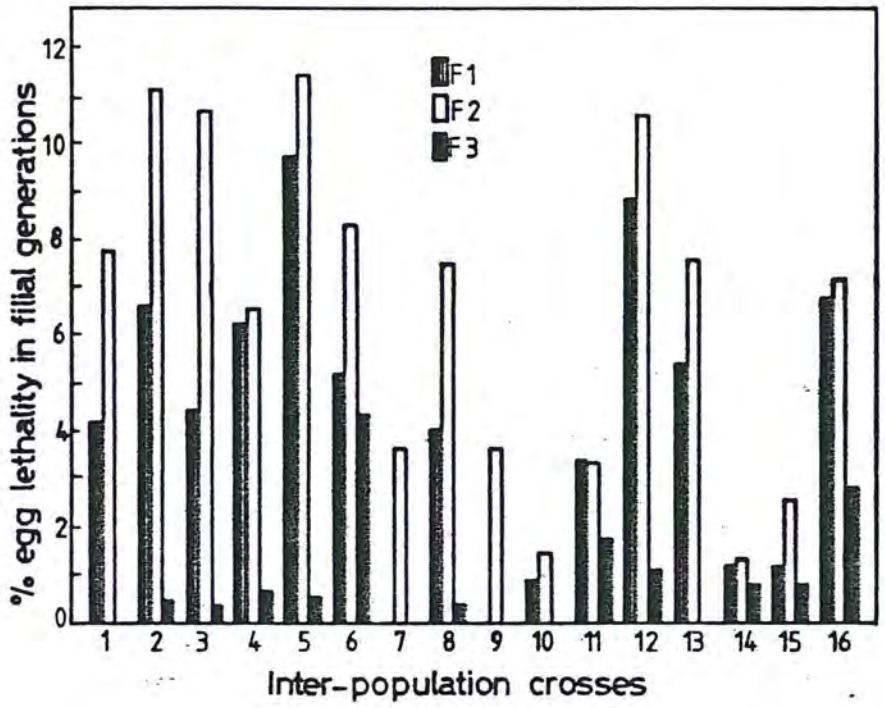

Fig. 3: Percentage egg lethality in inter-populational hybrid crosses between cassava green spider mite (CGM) populations from eco-climatic zones of Nyanza and Western Kenya.

Legend for Fig., 4

1. Rongo x Rusinga
2. Kibos x Rusinga
3. Kakamega x Rusinga
4. Siaya x Rusinga
5. Busia x Rusinga
6. Kibos x Rongo
7. Kakamega x Rongo
8. Siaya x Rongo
9. Busia x Rongo
10. Kakamega x Kibos
11. Siaya x Kibos
12. Busia x Kibos
13. Siaya x Kakamega
14. Busia x Kakamega
15. Busia x Siaya

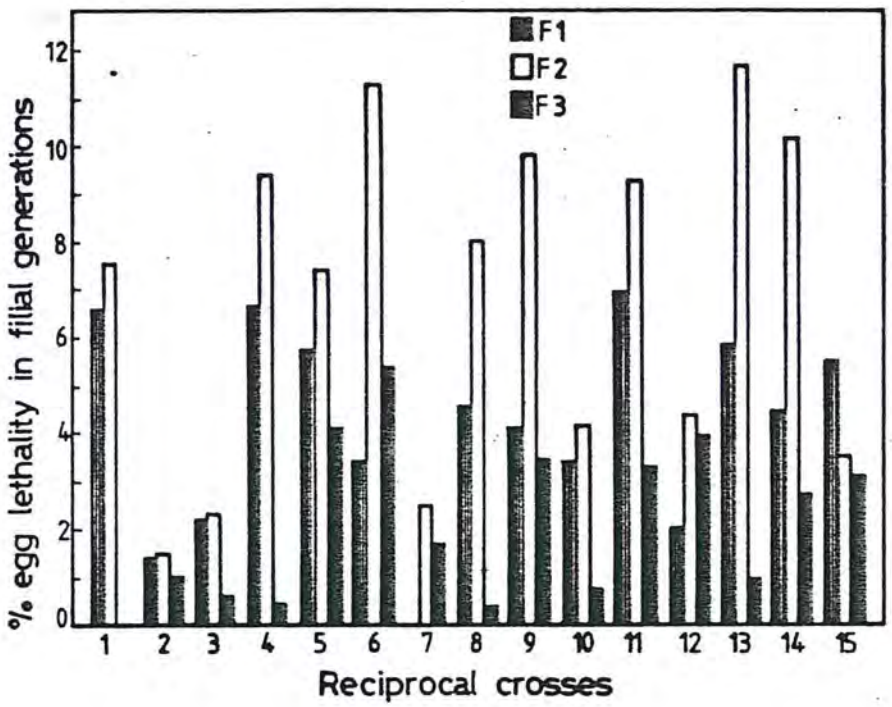

Fig. 4. Percentage egg lethality in reciprocal hybrid crosses between cassava green spider mite (CGM) populations from eco-climatic zones of Nyanza and Western Kenya

Legend for Fig., 5 (Inter-strain crosses)

1. Nairobi x Thika
2. Nairobi x Embu
3. Nairobi x Meru
4. Nairobi x Nyeri
5. Nairobi x Kitui
6. Nairobi x Machakos
7. Nairobi x Kimilili
8. Thika x Embu
9. Thika x Meru
10. Thika x Nyeri
11. Thika x Kitui
12. Thika x Machakos
13. Thika x Kimilili
14. Embu x Meru
15. Embu x Nyeri
16 Embu x Kitui
17. Embu x Machakos
18. Embu x Kimilili
19. Meru x Nyeri
20. Meru x Kitui
21. Meru x Machakos
22. Meru x Kimilili
23. Nyeri x Kitui
24. Kitui x Machakos
25. Kitui x Kimilili
26. Nyeri x Machakos
27. Machakos x Kimilili
28. Nyeri x Kimilili

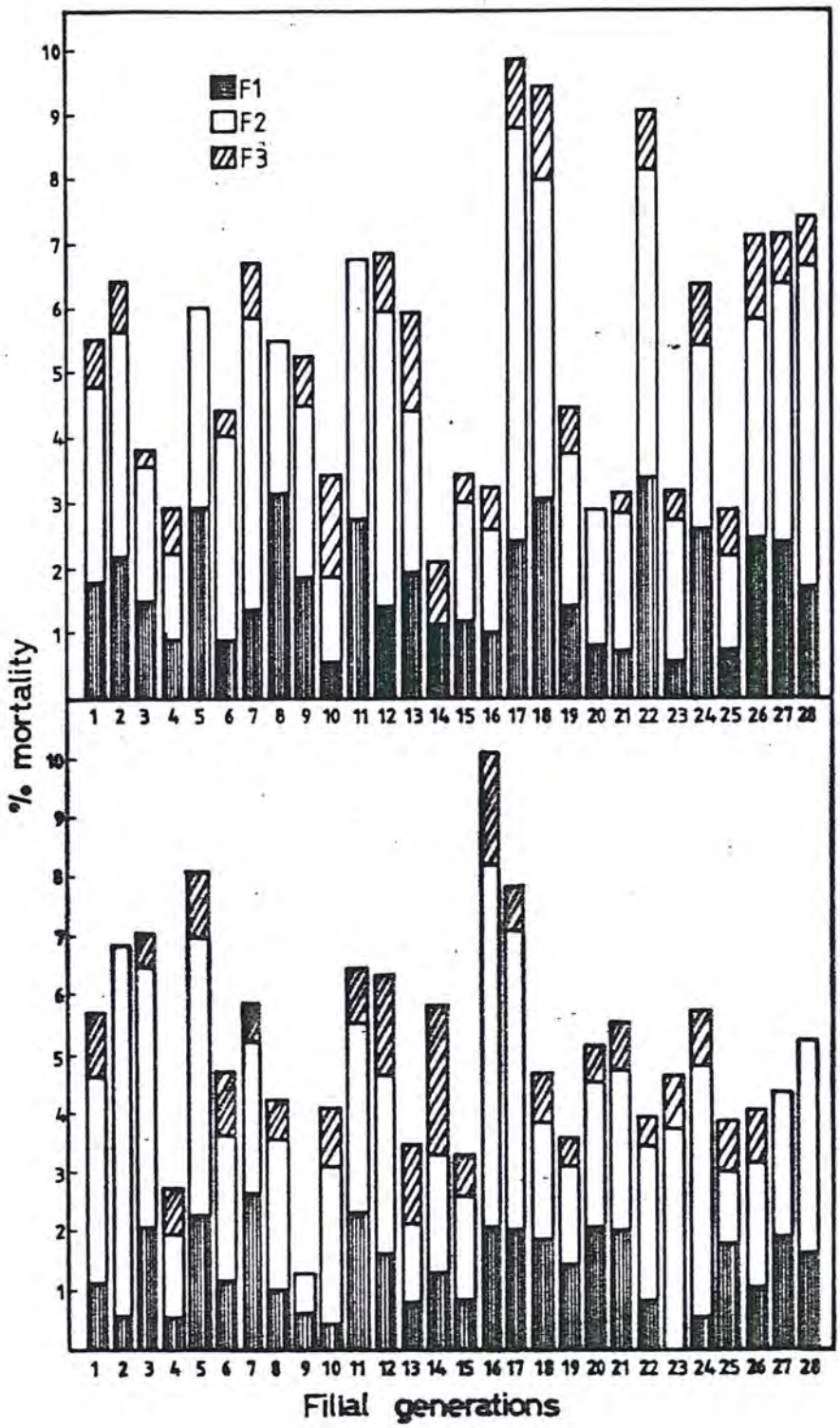

Fig. 5. Percentage diploid egg lethality in inter-populational hybrid crosses (top graph) and reciprocal hybrid crosses (second graph) between some cassava green spider mite (CGM) populations from eco-climatic zones of Eastern and Central Kenya

Legend for Fig., 6

1. Msambweni x Mvita
2. Msambweni x Mtwapa
3. Msambweni x Kilifi
4. Mvita x Kilifi
5. Mvita x Mtwapa
6. Mtwapa x Kilifi

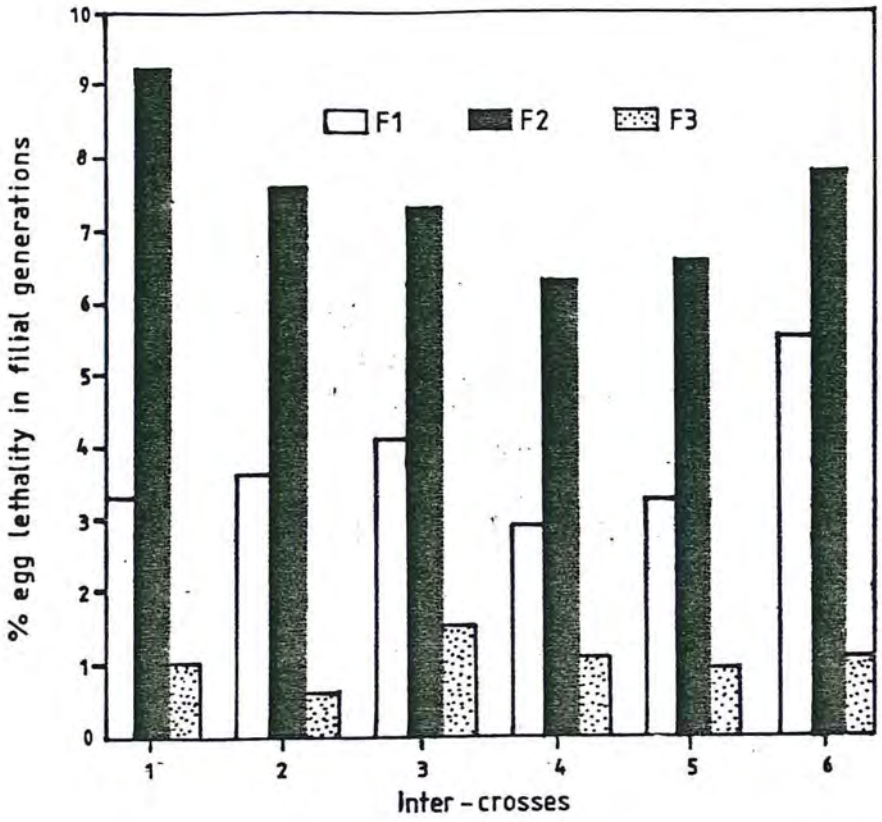

Fig. 6. Percentage egg lethality in inter-populational hybrid crosses between cassava green spider mite (CGM) populations from eco-climatic zone of the Coastal strip, Kenya

Legend for fig., 7

1. Mvita x Msambweni
2. Mtwapa x Msambweni
3. Kilifi x Msambweni
4. Kilifi x Mvita
5. Mtwapa x Mvita
6. Kilifi x Mtwapa

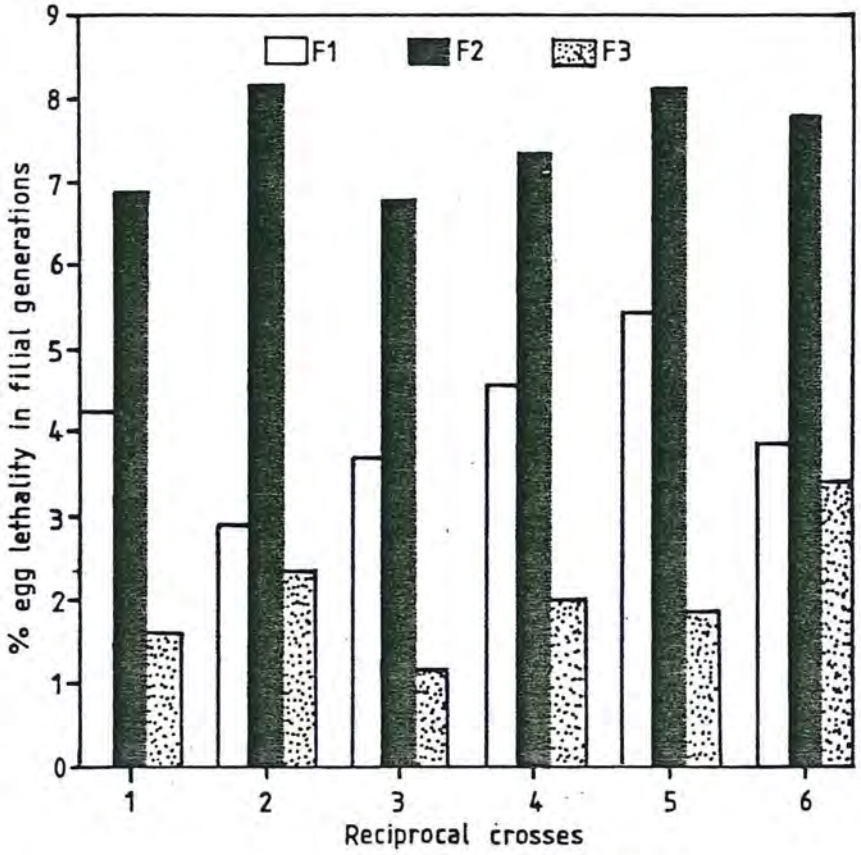

Fig. 7. Percentage egg lethality in reciprocal hybrid crosses between cassava green spider mite (CGM) populations from eco-climatic zone of the Coastal strip, Kenya.

Legend for Fig., 8

1. Meru x Msambweni
2. Meru x Kilifi
3. Meru x Isebania
4. Kitui x Msambweni
5. Kitui x Isebania
6. Isebania x Msambweni
7. Isebania x Kilifi
8. Isebania x Busia
9. Busia x Msambweni
10. Busia x Kilifi
11. Kitui x Kilifi

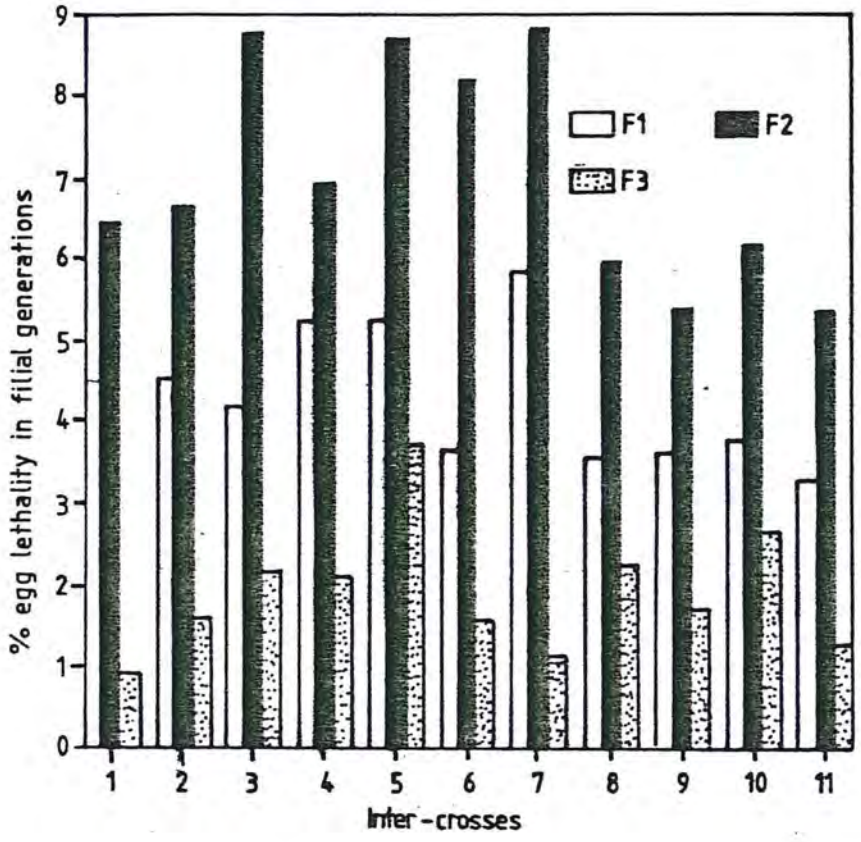

Fig. 8. Percentage egg lethality in inter-populational hybrid crosses between cassava green spider mite (CGM) populations from eco-climatic zone of the Coastal strip and up-country, Kenya

Legend for Fig., 9

1. Msambweni x Meru
2. Msambweni x Kitui
3. Msambweni x Isebania
4. Msambweni x Busia
5. Kilifi x Kitui
6. Kilifi x Meru
7. Kilifi x Isebania
8. Kilifi x Busia
9. Isebania x Meru
10. Isebania x Kitui
11. Busia x Isebania

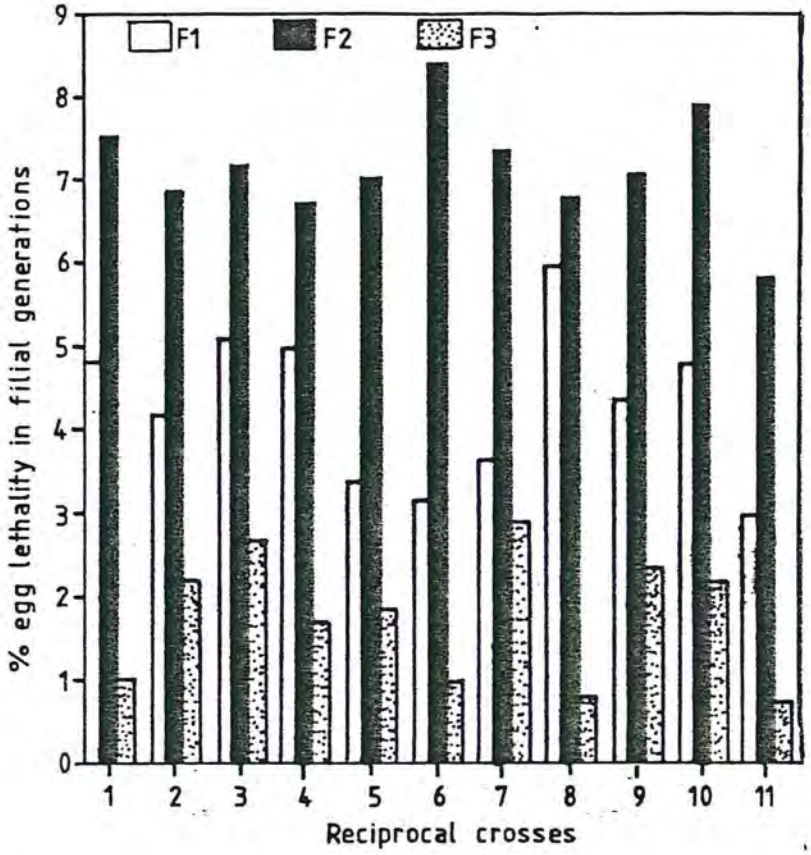

Fig. 9. Percentage egg lethality in reciprocal hybrid crosses between cassava green spider mite (CGM) populations from eco-climatic zone of the Coastal strip and up-country, Kenya.

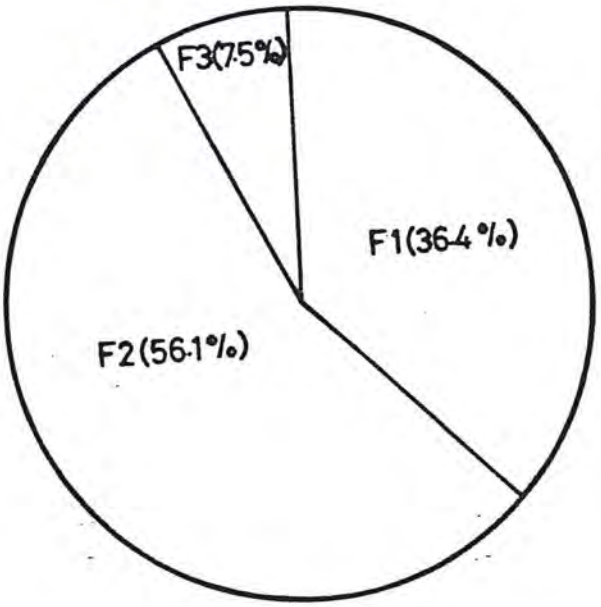

Fig. 10. Pie graph showing group mean percent egg lethality in three filial generations of inter-ppulational hybrid crosses of some cassava green spider mite (CGM) populations from eco-climatic zones of Nyanza and Western Kenya.

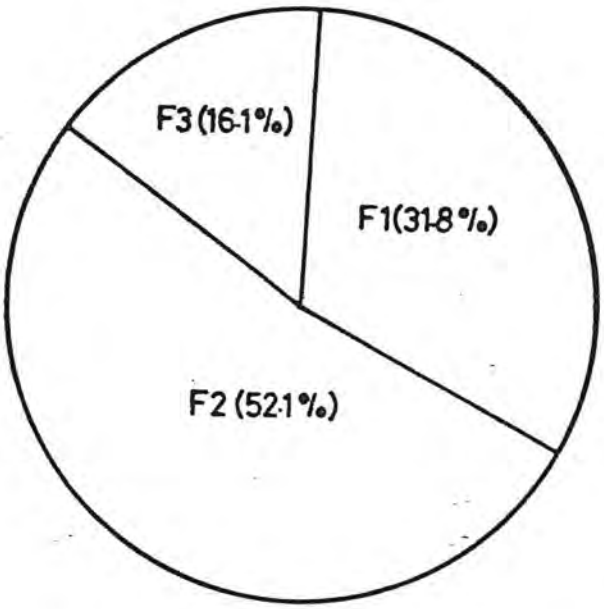

Fig. 11. Pie graph showing group mean percent egg lethality in three filial generations of reciprocal hybrid crosses of some cassava green spider mite (CGM) populations from eco-climatic zones of Nyanza and Western Kenya.

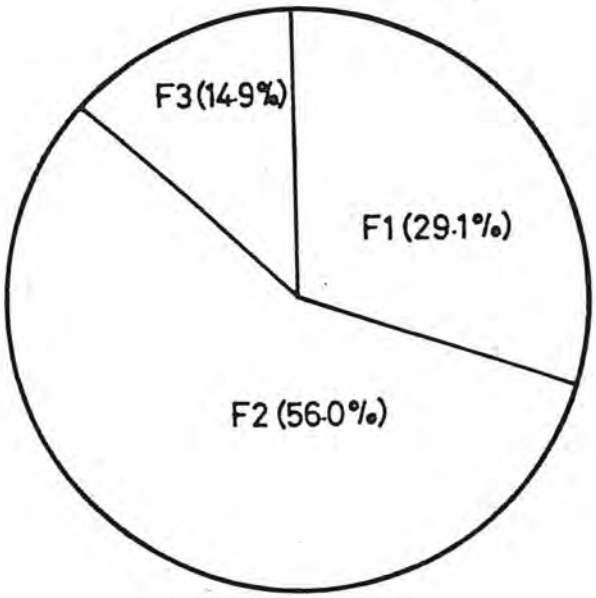

Fig. 12. Pie graph showing group mean percent egg lethality in three filial generations of inter-populational hybrid crosses of some cassava green spider mite (CGM) populations from eco-climatic zones of Eastern and Central Kenya.

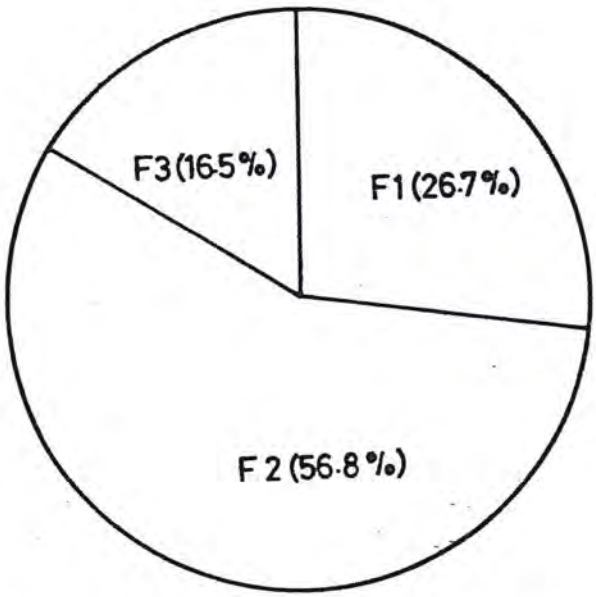

Fig. 13. Pie graph showing group mean percent egg lethality in three filial generations of reciprocal hybrid crosses of some cassava green spider mite (CGM) populations from eco-climatic zones of Eastern and Central Kenya.

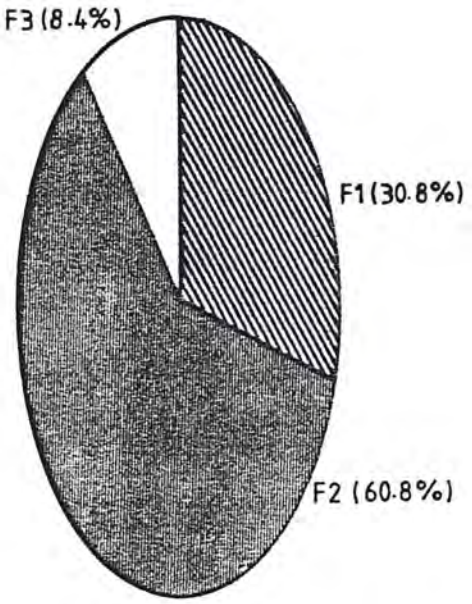

Fig. 14. Pie graph showing group mean percent egg lethality in three filial generations of inter-populational hybrid crosses of some cassava green spider mite (CGM) populations from eco-climatic zones of Coastal strip, Kenya.

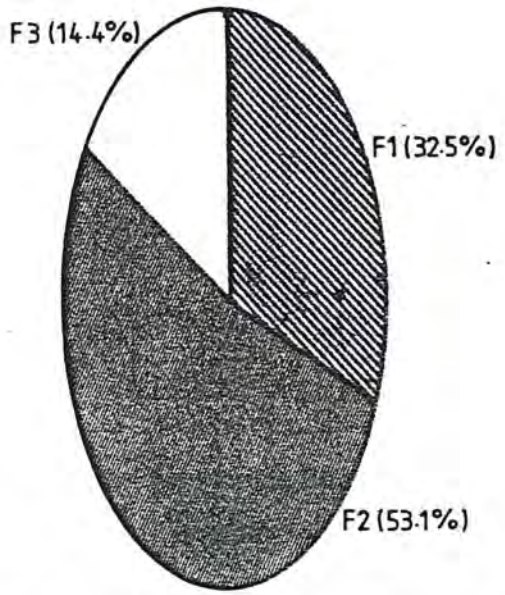

Fig. 15. Pie graph showing group mean percent egg lethality in three filial generations of reciprocal hybrid crosses of some cassava green spider mite (CGM) populations from eco-climatic zones of Coastal strip and up-country, Kenya.

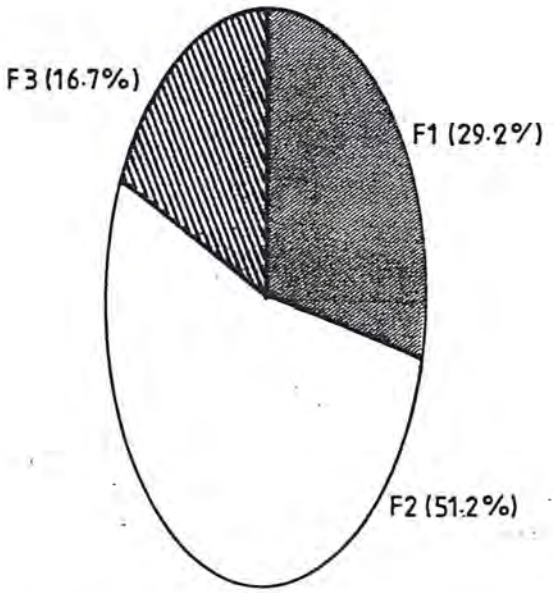

Fig. 16. Pie graph showing group mean percent egg lethality in three filial generations of inter-populational hybrid crosses of some cassava green spider mite (CGM) populations from eco-climatic zones of Coastal strip and up-country, Kenya.

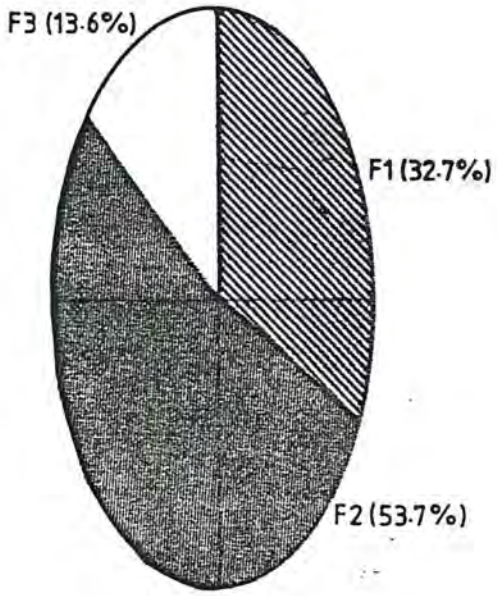

Fig. 17: Pie graph showing group mean percent egg lethality in three filial generations of reciprocal populational hybrid crosses of some cassava green spider mite (CGM) populations from eco-climatic zones of Coastal strip, Kenya.

4-5. Only the group filial mortality values over four "egg waves" gives meaningful overall group mean mortality values for F_1, F_2, and in F_3 progenies (Tables 2-5). As shown in Tables 2-9, the number of eggs laid differ among the inter-crosses and their reciprocals. This is surprising but as noted in the next section, the inviability of the eggs from the different crosses is a manifestation of partial hybrid sterility.

5.4 Discussion

A careful study of Tables, 3 and 5 and 7 and 9 and Figs., 4, 5, 7, 9, 11, 13, 15 and 17 shows that hybrids from reciprocal crosses had values markedly different among themselves as expressed in the degree of lethality mainly in the F_1 and F_2 eggs. This strongly suggests the effect of cytoplasmic factors. The differences in lethality among females of the same progeny and the improvement of fertility in subsequent generations was documented by Helle and van de Bund (1962) and Dosse (1963) among the T. urticae group populations. The data presented in these studies agree with the above observations as there are differences in crosses and their reciprocals and also enhanced F_3 fertility. de Boer (1980), is

of the opinion that this is not in agreement with Mendel's first law of inheritance, suggesting that non-Mendelian factors are involved. This is in perfect agreement with the data presented for *Mononychellus* in the present studies. The haploid egg lethality is caused by these extra-chromosomal factors which function like "genetic seive" in the elimination of deleterious gene recombinations from populations. Similar observations were made by Helle and van Zon (1967) and Overmeer and van Zon (1976) on spider mites of the *T. urticae* complex.

Fertilization in the F_2 (second backcross generation) partially restores the viability in eggs as is expressed in low F_3 percentage egg mortality values. As documented by Overmeer and van Zon (1976), this viability-restoring effect is enhanced through the sister X brother mating because the haploid brothers have inherited half the chromosomal complement of their mother thus propagating the genes of the original parental line. The partial sterility exhibited in these studies further suggests that this is due to the interaction between genes and cytoplasmic factors because as stated earlier deleterious genes are rapidly expelled from the population through the haploid sons. The viability restoring effect

becomes more evident if virgin daughters are mated with males from the original paternal line (de Boer, 1980). Although this line of argument was not persued in the current studies there is need for further investigations along this line.

Inter-populational partial lethality (Tables 2-9) means that complete sterility is lacking. The populations tested are, therefore, conspecific and share a common gene pool. According to Mayr (1969), species are groups of inter-breeding natural populations that are reproductively isolated from other such groups. Sailer (1954) stated that, "life forms" grade from freely inter-breeding populations through populations that are reproductively isolated in practice but still potentially capable of crossing and producing some fertile offspring to those that are incapable of interbreeding in any degree."

From the above statements, it is apparent that, the 19 populations investigated are in practice only reproductively isolated because of geographical distance as they are potentially capable of interbreeding and producing fertile offspring (F_1, F_2, and F_3). Sailer (1954), further, adds that fertile hybrids in the animal kingdom are unknown, but those that are formed e.g. in insects such as butterflies, moths,

drosophila and the mosquitoes or in mammals such as the mule, though viable are largely sterile and incompatible among themselves.

However, in spider mites, infertility may result from two definable isolation mechanisms, namely pre-zygotic and post-zygotic mechanisms. In pre-zygotic mechanisms spatial, behavioural and ecological isolation are capable of restricting the capacity to exchange genes, similarly, post-zygotic mechanisms act likewise in preventing gene exchange. Post-zygotic genetic isolation mechanisms include mechanical and gametic isolation, hybrid inviability, hybrid sterility and hybrid breakdown. In mechanical isolation, copulation is prevented because the aedeagus cannot fit in the female's vagina, while gametic isolation will ensure that no gamete fusion occurs despite copulation. Somehow, the sperms are inactivated or neutralized by substances in the female's reproductive system.

In post-zygotic isolation mechanisms hybrid inviability results due to disharmonious gene recombinations. High egg mortality (resulting from inability of chromosomes to pair during meiotic metaphase), is correlated with highly reduced fertility of any surviving daughters. If there are any surviving F_1 hybrids, they suffer

from hybrid sterility (de Boer,1980). Further success in F_1 hybrids is hampered by hybrid breakdown in the resultant F_2 progeny and extinction will result. To prevent wastage of such energy, pre- and post-zygotic isolating mechanisms have been devised in nature to prevent formation of such defective hybrid zygotes (cf Grant, 1966). In the case observed here fertile hybrids were formed (viable F_1, F_2 and F_3 hybrid progenies), signifying absence of these genetic isolation mechanisms.

From the data presented here (Tables, 2-9 and Figs., 3-17), it is very clear that among the populations hybridized, no pre-zygotic mechanisms exist as evidenced by successful mate finding which led to copulation, fertilization and formation of viable zygotes. The populations under study are, therefore, conspecific, they share a common gene pool as evidenced by their capacity to exchange genes.

Populations which have different gene pools tend to have different evolutionary tendencies (Crozier, 1985), but this is not the case here as the populations tested have so far not evolved into discreet species as they share the same gene pool, despite the low partial lethality shown. This is an indication of the absence of complete

reproductive isolation. This partial sterility is a feature common in most spider mites species (e.g. *Tetranychus urticae* group) whereby some form of partial lethality is found virtually between any two spider mite strains (Boudreaux, 1963; Helle and Pieterse, 1965; de Boer, 1980). It is very tempting to attribute the genetic differences noted among the CGM populations from Central and Eastern provinces to the effect of introgression of the Western and Nyanza CGM populations with those of the Coastal populations over this part of Central Kenya forming a diverse hybrid swarm.

However, no such differences were noted among Western and Nyanza CGM populations where introgression could equally occur between CGM populations from Uganda and those from the Central part of Kenya. The theory of the presence of introgressive hybrids in the Central part of the country is very plausible in view of the cultural practices carried out in this part of the country. The central part of the country is not a major cassava growing area and material planted here have been brought either from the coast or the west which would account for the introduction of CGM populations with diverse genetic make-up.

Natural hybridizations in such man-made situations would account for the observed genetic

differences whereby leakage of genes occur between such sub-populations. This divergent genetic make-up is also enhanced by the different eco-climatic zones from where these populations were collected. The eco-climatic zones range from arid Ithookwe (Kitui) to semi-arid Katumani (Machakos) to agriculturally high potential Runyenje's (Embu) and Maua (Meru) which differ considerably in temperature, relative humidity, rainfall and altitude (Fig. 2).

6.0 INTRA-POPULATIONAL COMPATIBILITY TESTS

6.1 Introduction

For the interpretation of hybridization data, it is important to know whether the test populations are inherently heterogeneous or uniformly homogeneous. This is because the intra-strain lethality values will reflect on the reliability of the inter-strain data as they serve as a check or control. The magnitude of egg lethality in such crosses is a good indicator of the variability in the populations being hybridized.

If there is a shift in the sex-ratio in favour of males as was reported by Helle and Pieterse (1965) on spider mites of the *Tetranychus* urticae group, usually results from a high lethality of the diploid eggs. This is reflected in the intra-strain egg lethality and is due to heterogeneity in colony composition. The present studies were initiated to find out the magnitude of this heterogeneity among the 18 CGM populations.

6.2 Materials and methods

The intra-strain egg mortality assessing the heterogeneity or homogeneity of the populations (check crosses) was studied for the 19 strains over 3 filial generations (G_1, G_2, and G_3). 10 partheno-produced males and 10 virgin females of each strain were placed on rearing leaf discs and G_1 generation eggs obtained. Mortality was scored 10 days later. The resultant progeny was reared to adulthood and 10, 15 day-old sib-mated females were further isolated for rearing of the G_2 progeny. Similarly, 10 15 day-old sib-mated females were used to produce G_3 generation (Tables, 10-12). In all cases 4 "egg waves" were made from which a mean on egg lethality for each cross was calculated.

Finally, the egg mortality data were subjected to statistical analysis (Gomez and Gomez, 1976) using the two way Anova (Appendices 10-12). Differences among the G_1, G_2, and G_3 filial progenies was assessed (Tables, 10-12; Appendices, 10-12).

6.3 Results

Check crosses (intra-population hybridization) (Tables, 10-12; Figs., 18-21), exhibited the pattern observed for inter-population hybridization such that egg mortality is lowest in the G_3 progeny compared to the G_1 ($G_1 < G_2 > G_3$; Appendices, 9-11; $p<0.0006$). Total pooled percent mortality in the three generations averaged slightly above 10, 30 and 50% for the three generations (G_1, G_2 and G_3) respectively (Figs., 21-23). However, for intra-crosses from Central Kenya (Table, 11; Fig., 19 and 22), there were seemingly no differences between G_1 and G_3 egg lethality (Appendix, 10). The G_2 showed the highest percentage egg mortality of 15.80 for Isebania populations in the Nyanza eco-climatic zone while the lowest was 1.05% for Kakamega populations in the Western eco-climatic zone (Tables, 10 and 12; Fig., 18). However, when tested statistically (Appendices, 9-11), significant differences were found between progeny generations (G_1, G_2 and G_3) ($p<0.0001$).

The difference between group egg mortality among the three generations were statistically significant when compared among the

Table 10. Intra-populational check crosses in three filial generations (G_1, G_2 and G_3) of some CGM populations collected from Nyanza and Western, Kenya.

Collection Site	% Egg lethality (No. of eggs laid in brackets)			Sex-ratio (Female:male)		
	G_1	G_2	G_3	G_1	G_2	G_3
Rusinga	6.93(101)	10.45(268)	0.00(155)	3:1	3:1	3:1
Rongo	6.38(141)	7.23(235)	0.66(152)	2:1	2:1	5:1
Kibos	7.39(230)	8.43(332)	1.23(243)	2:1	3:1	4:1
Kakamega	3.79(395)	1.05(286)	0.00(399)	4:1	3:1	2:1
Siaya	6.29(159)	10.57(227)	3.47(173)	3:1	4:1	3:1
Busia	0.35(289)	5.29(170)	1.34(299)	4:1	3:1	2:1
Kimilili	1.25(321)	1.35(371	0.56(359)	3:1	3:1	2:1
Isebania	9.80(183)	15.80(133)	7.55(172)	3:1	2:1	2:1

Table 11. Intra-populational check crosses of some CGM populations from Eastern and Central eco-climatic zones.

Check cross	% Egg lethality (No. of eggs laid in brackets)			Sex-ratio (Female:male)		
	G_1	G_2	G_3	G_1	G_2	G_3
Nairobi	1.72(174)	4.55(132)	0.98(407)	3:1	3:1	2:1
Thika	1.64(183)	1.92(260)	0.39(258)	2:1	1:1	3:1
Embu	3.43(175)	3.33(270)	0.66(456)	5:1	2:1	3:1
Meru	1.39(216)	4.64(151)	0.00(398)	2:1	2:1	2:1
Nyeri	2.46(122)	4.95(182)	2.18(275)	3:1	4:1	3:1
Kitui	1.03(195)	2.15(233)	1.90(263)	2:1	2:1	1:1
Machakos	2.28(438)	8.51(94)	0.00(151)	3:1	3:1	3:1

Table 12. Intra-populational check crosses in three filial generations (G_1, G_2 and G_3) of some CGM populations collected from Coastal eco-climatic zone.

Check cross	% Egg lethality (No. of eggs laid in brackets)			Sex-ratio (Female:male)		
	G_1	G_2	G_3	G1	G2	G3
Msambweni	3.50(290)	8.11(163)	1.27(240)	2:1	2:1	2:1
Mvita	4.14(119)	7.63(191)	2.31(278)	2:1	2:1	2:1
Mtwapa	3.43(174)	6.76(154)	1.17(275)	2:1	2:1	2:1
Kilifi	3.64(140)	7.73(186)	2.62(311)	2:1	2:1	2:1

G_1= Generation 1

G_2= Generation 2

G_3= Generation 3

Lengend for Figure., 18

1. Rus= Rusinga
2. Rgo= Rongo
3. Kbs= Kibos
4. Kak= Kakamega
5. Sya= Siaya
6. Bsa= Busia
7. Kim= Kimilili
8. Isb= Isebania

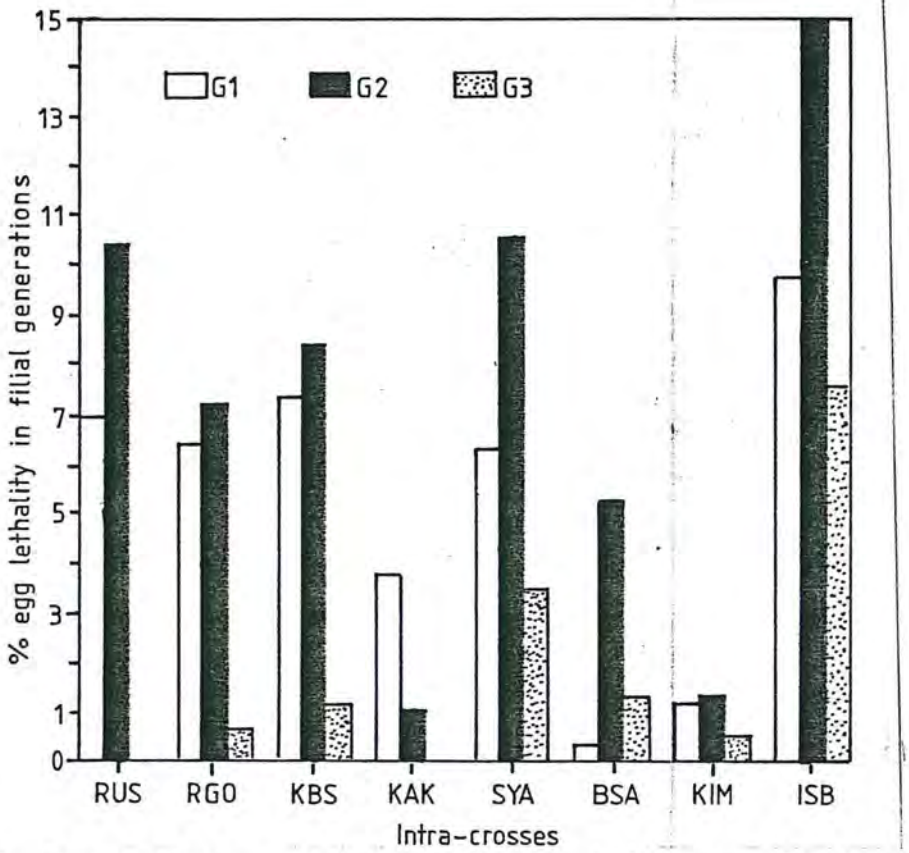

Fig., 18. Percentage egg lethality in intra-populational hybrid crosses between cassava green spider (CGM)populations from eco-climatic zones of Nyanza and Western Kenya

1. Nbi=	Nairobi	2. Tka=	Thika
3. Emb=	Embu	4. Mer=	Meru
5. Kit=	Kitui	6. Mks=	Machakos

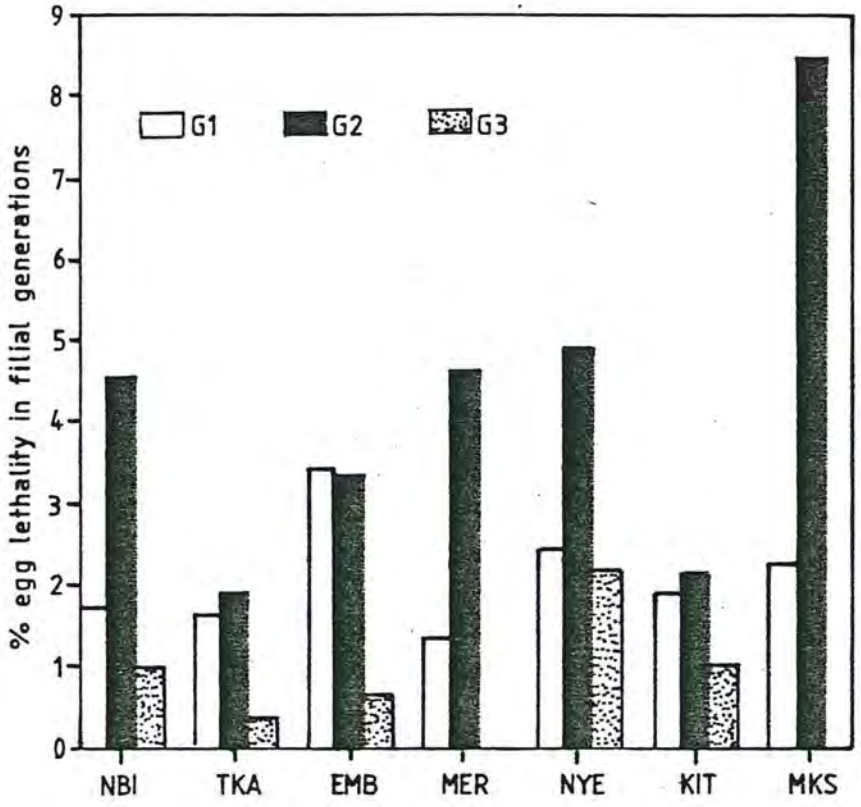

Fig. 19. Percentage egg lethality in inter-populational hybrid crosses between cassava green spider mite (CGM) populations from eco-climatic zones of Eastern and Central Kenya

1. Msb= Msambweni
2. Mvt= Mvita
3. Mtp= Mtwapa
4. Klf= Kilifi

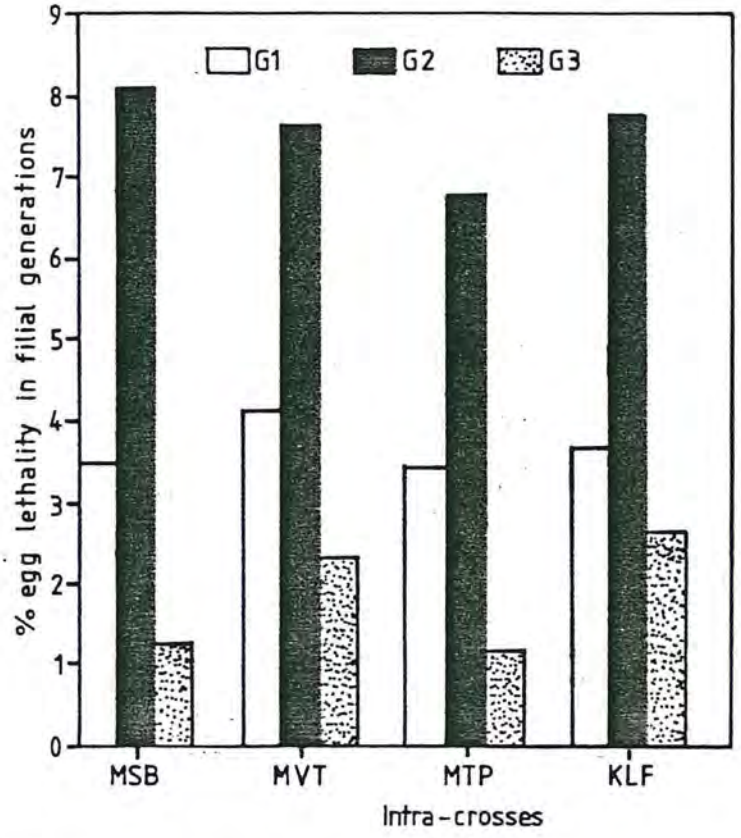

Fig. 20. Percentage egg lethality in intra-populational hybrid crosses between cassava green spider mite (CGM) populations from eco-climatic zone of the Coastal strip, Kenya.

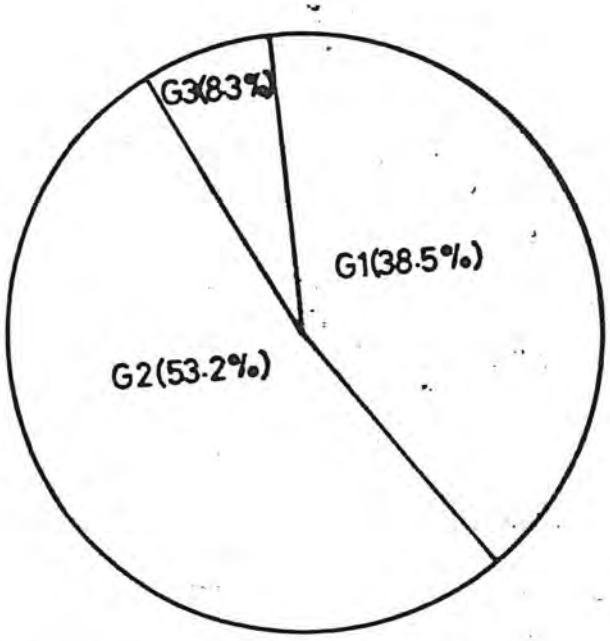

Fig. 21. Pie graph showing group mean percent egg lethality in three filial generations of intra-populational hybrid crosses of some cassava green spider mite (CGM) populations from eco-climatic zones of Nyanza and Western Kenya.

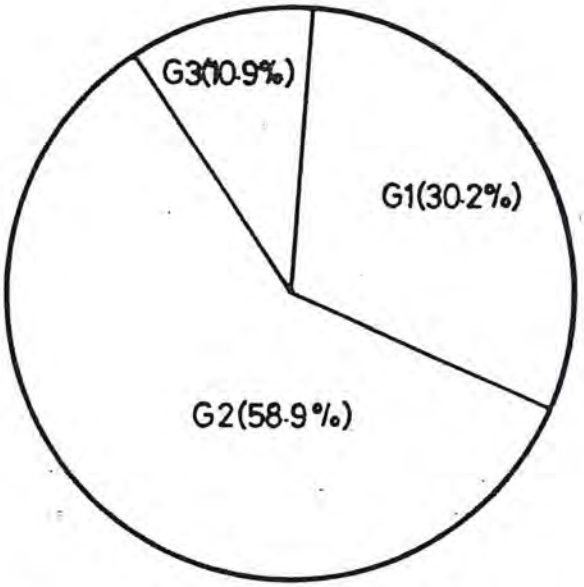

Fig. 22. Pie graph showing group mean percent egg lethality in three filial generations of intra-populational hybrid crosses of some cassava green spider mite (CGM) populations from eco-climatic zones of Eastern and Central Kenya.

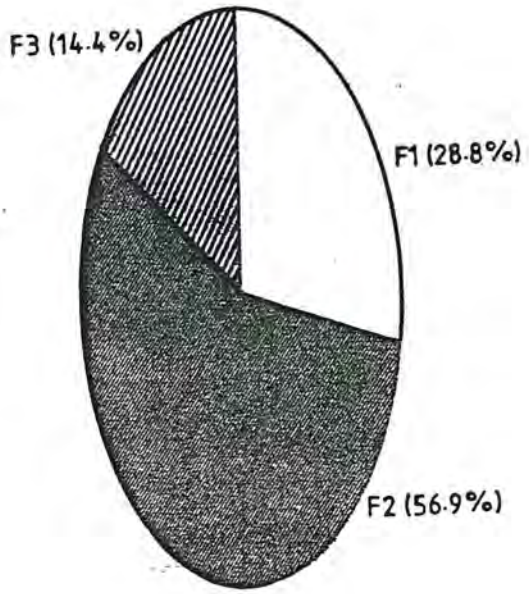

Fig. 23. Pie graph showing group mean percent egg lethality in three filial generations of intra-populational hybrid crosses of some cassava green spider mite (CGM) populations from eco-climatic zones of Coastal strip, Kenya.

19 sampling sites from which the intra-crosses were made ($p<0.05$; Tables,10-11; Appendices, 9-11). Group mortalities between G_1, G_2 and G_3 were statistically different in populations from Nyanza and Western Kenya (group means = 1.140, 2.709 and 2.298 respectively) and populations from the Coast (Group means = 1.943, 2.767 and 14.640, respectively) ($p<0.0001$; Appendices, 9 and 11) while those from Central Kenya group means for G_1 (1.359) and G_3 (1.042) were not significantly different from each other but were different from those of the G_2 (group means = 1.879) ($p<0.0006$; Appendix, 10). The least heterogeneity was recorded in the G_2 (group means = 1.879; $p<0.0006$; Appendix, 10). The least heterogeneity was recorded in the G_3 where values of the order of 0.00% were common (Tables, 10 and 11). From the overall lethality means, the populations from the Coast and Nyanza and Nyanza Kenya (Tables, 9-11). Perhaps the most significant observation made during these studies concerns the statistical test for the interaction between filial generations and the sites from which the mites were obtained among the five eco-climatic zones. As shown in Appendices 9-11, this interaction was not significantly different ($p>0.05$), meaning that the CGM populations investigated are not genetically

different.

6.4 Discussion

The implication of the above results (Tables, 10-12; Figs., 18-23 and Appendices, 9-11) is that the populations tested were heterogeneous in their composition, since intra-crosses are expected to have very low (if not nil) lethality values. This is a feature which has been tested and observed in other tetranychid mites notably the *Tetranychus urticae* group (van de Bund and Helle, 1960; Helle and van de Bund, 1962) where intra-strain check mortalities were below 10%. In the present studies, most of the average intra-strain mortality values (Tables, 10-12) fall below this value. This observable significant mortality in intra-strain hybrids points to the existence of intra-populational differences inherent in the test populations (intra-hybrid differences). Factual evidence of zygotic development is supplied by Tables, 10-12, implying that successful copulation and fertilization were accomplished, although partial sterility in the intra-crosses was obtained. The heterogeneity reported here conforms to similar observations made by Helle and Pieterse (1965) on *T. urticae*

group who observed that heterogeneity is a common feature in spider mites resulting from accelerated differentiation in genome composition as a result of the short mean generation time and the male haploidy. Boudreaux (1963), was of the opinion that this heterogeneity (semi-incompatibility) may result from chromosomal sterility due to failure of pairing and disjunction in meiosis causing genome defficiency and thus death in the resultant progeny.

It is in this context that the divergent sub-populations reported from Central Kenya should be viewed. These sub-populations although divergent are still capable of exchaging genes because they share a common gene pool. The sub-specific differences observed in test crosses from Central Kenya (Chapter 5) were not confirmed by control (check) crosses. This implied that the differences observed between the filial generations and the sites (interaction) were most probably a result of extra-chromosomal factors (cf. de Boer, 1983).

The populations hybridized were genetically alike despite the observed partial hybrid sterility. This is supported by the statistical tests (Appendices, 9-11) which show that although the CGM exhibits heterogeneity, as

expressed in the partial intra-strain hybrid sterility, the populations tested despite being geographically isolated are genetically the same. Allopatricity, therefore, has not led to the formation of distinct species status as would be expected. This partial sterility is expected and is a common feature among spider mites because as noted by de Boer (1980), any two strains of spider mites including laboratory strains can develop similar partial inter-breeding barriers.

7.0 SEX INHERITANCE AND SEX-RATIO STUDIES

7.1 Introduction

Spider mites are usually bisexual and reproduce by arrhenotokous parthenogenesis. This implies that a fertilized female will give rise to both diploid daughters and haploid sons while if unfertilized an exclusive male progeny results (de Boer, 1979). In a normal sex-ratio, a prepoderance of females results giving an average ratio of 3:1 (Overmeer, 1967; Overmeer and Harrison, 1969)).

The frequency of fertilization of the eggs determine the sex-ratio and is a reflection of the efficiency of the spermathecal gland to release sperms. Since this is genetically controlled by the female, it may reflect the level of sexual compatibility between test populations as the frequency of diploid eggs in a test progeny is a manifestation of their phylogenetic proximity (Overmeer and Harrison, 1972). Three types of sex-ratios are distinguishable namely, the primary, secondary and the tertiary sex-ratios. The primary sex-ratio is the ratio of the mites at oviposition while the secondary sex-ratio is the ratio at adult eclosion from the deuto- or tritonymph. The

tertiary sex-ratio is the ratio in adults of undetermined age in the field (Proctor, 1989). In the present studies it is the secondary sex-ratio that was scored.

7.2 Materials and methods

To verify whether MononychellusF conforms to arrhenotokous parthenogenetic mode of sexual reproduction, single virgin females representing strains from the six selected sites were isolated on leaf discs (diameter ca 1.8 cm) and allowed to oviposit for 48 hours and the number of eggs produced recorded. Final hatchability was scored 10 days later. The offspring were allowed to mature and the resultant siblings sexed (Tables, 13-15). Also secondary sex-ratios of hybridized populations and their reciprocal crosses (Tables, 2-12) were scored.

7.3 Results

From the data presented (Tables, 13-15), it is shown that Mononychellus sp.F reproduces by arrhenotokous parthenogenesis. This is because an exclusive haploid generation was produced by

unmated females from the 19 sites collected from the five ecological zones. As expected the virgin females laid only a few eggs (de Boer, 1980), the highest being 9 (Table, 13-15). The eggs suffered some mortality, the highest being 42.86% for eggs from a virgin female from Machakos (Table, 14). Little significance should be attached to the seemingly high percent haploid lethality. This is because as observed (Tables, 13-15), the number of eggs laid is exceedingly small which give artificially high lethality values on calculation. The small number of eggs laid is expected and is a survival mechanism among many spider mite species such as *T. urticae* (de Boer, 1980). In the sex-ratio studies, the ratios varied from 1:1 (female:male) to as high as 8:1. Hybrid populations from Nyanza, Western and Central had high sex-ratios signifying that fertilization was more successfull but there was a high mortality in haploid eggs. The average ratio recorded was 3:1 (Tables, 2-5) compared to the Coastal populations where the highest sex-ratio was 3:1, and the average being 2:1 (Tables, 6-9). These low sex-ratios are reflected in the level of incompatibility which is lower in hybrid populations from Eastern, Central, Nyanza and Western (Tables, 2-5) compared to higher

Table 13. Arrhenotoky check for CGM populations from Nyanza and Western Kenya.

Population Sampled	No. of eggs laid	No. of eggs hatched	% haploid lethality	Secondary sex-ratio
Busia	7	6	14.29	All males
Siaya	8	6	25.00	"
Kakamega	6	4	33.33	"
Kibos	9	7	22.22	"
Rongo	5	5	0.00	"
Rusinga	8	7	12.50	"
Kimilili	7	5	28.60	"
Isebania	4	3	25.00	"

Table 14. Arrhenotoky check for CGM populations from Central Kenya.

Population	No. of eggs laid	No. of eggs hatched	% haploid lethality	Secondary sex-ratio
Nairobi	8	7	12.50	All males
Thika	7	5	28.57	"
Nyeri	9	9	0.00	"
Embu	6	5	16.67	"
Meru	5	4	20.00	"
Machakos	7	4	42.86	"
Kitui	8	6	25.00	"

Table 15. Arrhenotoky check for CGM populations from Coast Province, Kenya.

Population Sampled	No. of eggs laid	No. of eggs hatched	% haploid lethality	secondary sex-ratio
Kilifi	8	8	0.00	All males
Mtwapa	7	6	14.28	"
Mvita	9	6	33.33	"
Msambweni	6	4	33.33	"

incompatibility levels in crosses derived from populations from the Coast and a combination with up-country populations (Tables, 6-9).

7.4 Discussion

The parthenogenetic mode of reproduction is useful in the interpretation of hybridization data because spider mites are bisexual and exhibit arrhenotoky. The males in arrhenotokous species are therefore "fatherless", impaternate or uniparental having inherited half the genome (n=3) of their diploid mothers (2n=6). In such haplo-diploid systems, the males are hemizygous and all the genes act like dominants (Bruickner, 1975). The sperms have identical genotypes to the males producing them, deleterious genes, therefore, do not accumulate in such systems (Hartl, 1971). In the present studies, it was shown that due to the haploid nature of *Mononychellus* males, deleterious genes do not accumulate and are rapidly expelled from the system as is reflected in the haploid egg lethality resulting in high sex ratios in favour of females (Tables, 2-12).

However, when de Boer and Oreel, (1980), crossed an F_1 female with a male derived from the original female parental line of the *T. urticae*

group they showed that the resultant lethality in the non-hybrid sons was caused by factors localized in the cytoplasm (non-Mendelian factors). The lethality recorded in the present studies was attributed to cytoplasmic factors as no hybridization took place and therefore no exchange of genes was involved. Chromosomal inheritance in the haplo-diploid system is very unique as females are biparental. A cross fertilized female gives rise to hybrid F_1 daughters and non-hybrid sons, the latter being of the maternal genotype. From the foregoing, F_1 males are non-existent, brother x sister mating gives a first backcross generation of the daughters (not F_2), (de Boer, 1980). This information was found useful in interpreting both the intra- and inter-strain hybridization data. The absence of females indicate that the males were produced by arrhenotokous parthenogenesis.

Helle (1967), observed that the first eggs produced by a mated female is always male determined as sperms do not reach it in time. Later on, more eggs escape fertilization despite sufficient sperms. The mechanism by which the female "decides" when to release the sperms stored in the spermathecal gland is poorly understood (Crozier, 1985; Helle and Pijnacker, 1985)

although earlier, Mitchell (1972) had suggested that this may be genetically determined. This is not surprising because if only diploid eggs were produced, progeny extinction would result as no males would be available for inseminating the females (Putman, 1970). It is for this reason that virgin females conserve energy by laying fewer eggs so that they live longer than mated ones (de Boer, 1980). This low number of eggs averaging 7.05 per female per site (Tables, 13-15) compared to 16.61 per fertilized female per test-cross (F_1 generation; Table, 2) ensures that haploid sons will mature and mate with their diploid mothers and therefore, avert genetic death. The sex allocation theory propounded by Goldschidt in 1934 whereby males in bees are determined by extra-chromosomal factors and females by interaction of cytoplasmic and chromosomal factors needs further investigation. As far as maleness in spider mites is concerned Helle and Overmeer (1973) believe that similar mechanisms operate in mites but this seems to be far fetched in light of the evidence presented here which show that males are maternally derived through arrhenotokous parthenogenesis.

Although the virgin females produced eggs from which an exclusive male progeny

developed (Tables, 13-15), this cannot be conclusively proved to be arrhenotoky from the data presented (cf. Helle and Pijnacker, 1985). From the definitions of the various terms on arrhenotoky (discussed in 2.5), it is difficult to distinguish haploid parthenogenesis (arrhenotoky), pseudo-arrhenotoky and gynogenetic arrhenotoky from genetic data alone (Helle *et al.*, 1981; Helle and Pijnacker, 1985). This can only be confirmed through analytical studies of mitotic chromosomes in embryonic or egg squashes (Helle and Bolland, 1967; Helle *et al.*, 1970; Gutierrez *et al.*, 1979; Nelson-Rees *et al.*, 1980; Helle and Gutierrez, 1983). Cases of bisexual spider mites which give males by arrhenotoky are well documented through karyotype analysis (Helle *et al.*, 1970; Gutierrez *et al.*, 1979). In the current studies, the CGM populations tested were regarded as arrhenotokous. This was based on indirect evidence from hybridization data and on an earlier unpublished karyotype study by the author in the laboratory of Applied Entomology at the University of Amsterdam where it was established that the haploid and the diploid chromosome numbers for CGM populations from Kenya were 3 and 6 respectively. From the foregoing, it can be stated with a significant level of certainity that the CGM populations

tested exhibit arrhenotoky.

Wrensch and Young (1975), reported that in the colonizing phase, the number of female siblings available for dispersal will determine reproductive success. This implies that the sex ratio should be biased towards the females. Extreme deviations from the "normal" sex ratio which may be as high as 9:1 (Wrensch and Young, 1978), may indicate some underlying genetic abnormalities such as deleterious recessive genes occuring during gamete formation. In such cases the sex-ratio will reveal a high number of females as males act as path-ways ("genetic seives") in elimination of such deleterious genes in haplo-diploid organisms (Helle and van Zon, 1967). This is well represented in Tables, 2-5, showing values from Eastern, Central, Nyanza and Western Kenya where sex-ratio values are high (highest sex-ratio being 8:1).

The so called "normal sex-ratio" for spider mites is 3:1 (Laing, 1969; Overmeer, 1972). The sex-ratio is genetically determined (Mitchell, 1972) and is influenced by maternal effect (Overmeer and Harrison, 1969), length of copulation (Overmeer and Harrison, 1972) and the nature of developmental environment and population density (Wrensch and Young, 1978). These sex-

ratios are, therefore, good indicators of the proportion of the eggs fertilized (cf. Helle, 1967). The high sex-ratios reflect successful hybrid formation and, by inference the level of phylogenetic proximity of the populations. Failure of fertilization results in an exclusive haploid generation (sons) giving a distorted sex-ratio. A strain may become extinct when procreation is terminated. This was witnessed in the present studies (Tables, 13-15) because only males were produced and were prevented from mating with their mothers as these were removed.

The sex-ratio values recorded were in favour of females (Tables, 2-9). This proves that fertilization occurred as evidenced by hybrid formation (diploid females). Normal gamete formation occurred but the high female/male ratios indicates occurrence of haploid mortality or that a greater proportion of the eggs produced were fertilized. This is not surprising because as already stated deleterious genes are eliminated in the haploid phase .

The evidence presented in the current studies indicates that the populations hybridized consists of one species. This is because the populations were found to interbreed as shown by the sex-ratios which reflects the high degree of

fertilization as shown by the large number of hybrid daughters produced. Since the species is arrhenotokous and the males inherit half the genome of their mother they are, therefore (males), of the same species as their mothers. Since neither abnormal nor distorted sex-ratios were detected in the test crosses, there were no pre- or post-zygotic isolation mechanisms. In the first case, attempted copulation may occur but is unsuccessfull as the females become irritable and move away or structural differences in the copulatory organs will not allow penetration by the male. In the latter case, copulation with or without fertilization may occur and in the second case, the resultant hybrid dies in the embryonic stage. If it survives, no progeny is produced or a heterotic sterile female is produced. Such levels of attempted hybrid formation is a manifestation of the phylogenetic proximity of the test populations. Among the 19 different geographical populations, genetic isolation mechanisms were absent as revealed by the high degree of fertilization and formation of hybrid zygotes. This is reflected in the sex-ratios which show a preponderance of hybrid female siblings.

8.0 GENETIC INHERITANCE OF DORSO-CENTRAL HYSTEROSOMAL SETAE

8.1 Introduction

The envisaged biological control measures for the CGM which has now spread in the whole of the cassava belt in sub-saharan Africa relies on the importation of exotic predators from the CGM's original topotype (Herren, 1984; Megevand *et al.*, 1987). However the success of this programme is dependent on the exact identity of the CGM whose present taxonomic status is in a state of confusion (Gutierrez, 1987).

In Africa, two species identified on the basis of the morphological criteria are *Mononychellus tanajoa* (Bondar) and *M. progresivus* Doreste (Flechtmann, 1981; Doreste, 1982). The classical morphological method used to distinguish the above two species (MacFarlane, 1984) has been based on the length and position of dorso-central hysterosomal setae in relation to their longitudinal distances (D_1-D_2 and D_2-D_3) between their bases (Plate, 6; Fig., 24). From this description, *M. tanajoa* is described as having its D_1-D_2 approximately egual in length which is less

than half the distance to the next. In M. *progresivus*, the dosal setae length are unequal in length such that $D_3 > D_2 > D_1$, but the D_2 and the D_3 setae are about $^2/_3$ as long as the distance to the next.

However, recent indications are that perhaps one species occurs (Gutierrez, 1987). Evidence for the presence of a somewhat variable non-homodynamic species has been shown through hybridization studies among Kenyan CGM populations is presented in chapter 5 and through discriminant function analysis of females dorsal setae (Nokoe and Rogo, 1988; Bob-Manuel, 1988) and iso-enzyme electrofocussing (Oyugi, 1989). It is noteworthy also that the aedeagii of all the CGM males examined from Africa show the species to be M. *progresivus* (Rogo *et al.*, 1987).

The aim of the present studies was to elucidate the taxonomic status of the CGM using hybridization data, and to discount through genetic evidence the invalidity of the female's dorso-central hysterosomal setae for species diagnosis.

8.2 Materials and methods

For the purposes of the present studies, 6 sites were selected from the 19, representing a

cross-section of the cassava growing areas of Kenya. This cross-section was a transect taken in an approximately North-West to a South-East direction from the Kenya-Uganda border at Alupe (Busia) to the Kenyan coast at Msambweni (South Coast), a distance of approximately 1,000 km (Fig. 1).

The sites were selected are: Msambweni (south coast) (Coastal eco-zone), Ithookwe (Kitui) (Eastern eco-zone), Runyenje's (Embu) (Central eco-zone), Alupe (Busia) (Western eco-zone), Ran'gala (Siaya) and Kamasengre (Rusinga island) (Nyanza eco-zone), (Fig. 1).

Rearing of the mites was accomplished using the cassava leaf disc technique devised for *Mononychellus* by Murega, (1989). 10 virgin females and males were paired from each of the selected six sites and allowed to oviposit for 48 hours after which the founder male and female parents were removed and preserved in 70% alcohol to be mounted later. 10 days after oviposition, all the viable eggs had hatched. The F_1 larvae were then transferred onto fresh leaf discs and allowed to develop to maturity.

A fully developed F_1 progeny was obtained on day 15. The founder parents (n=12) as well as F_1 females (n=180) and males (n=10) were mounted

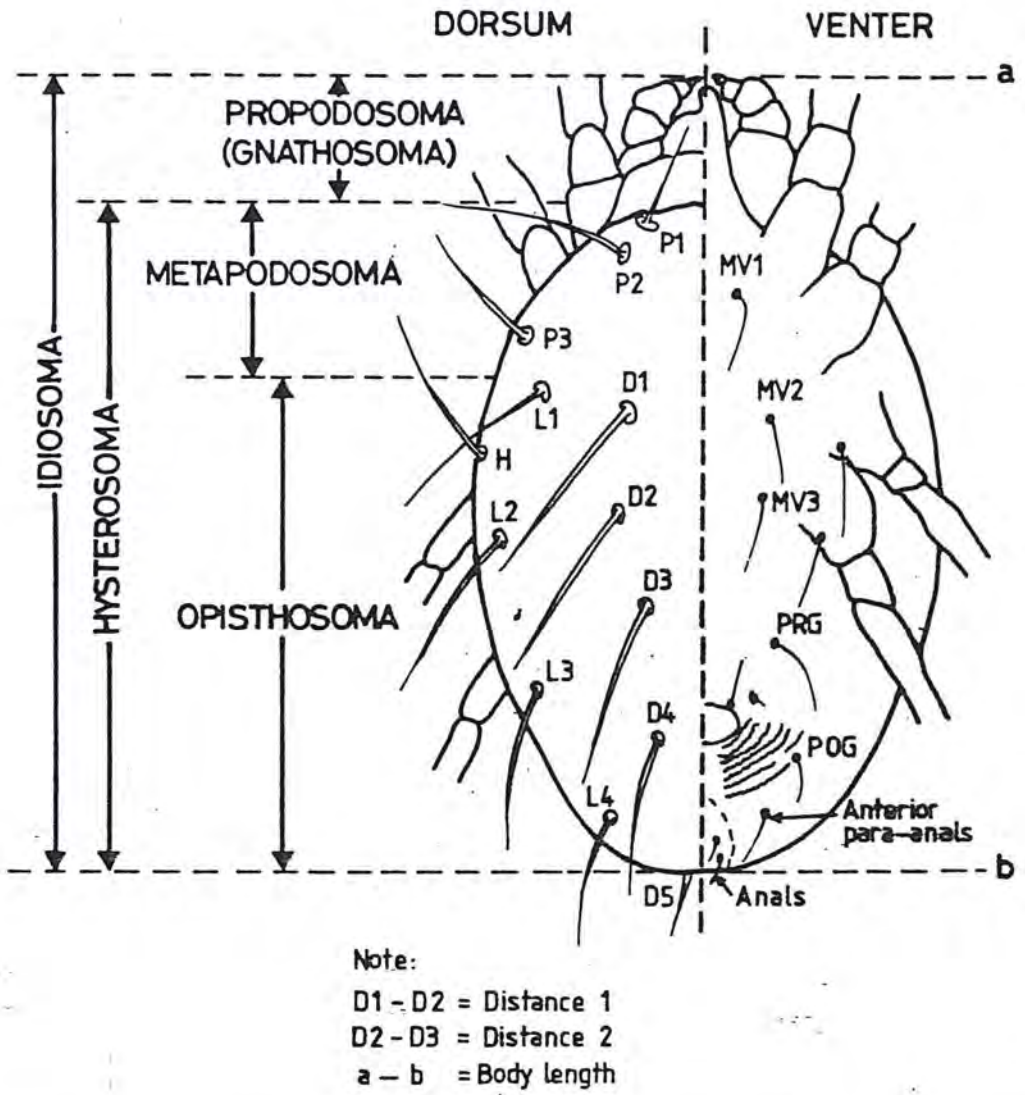

Fig. 24 : A general view of a Tetranychid spider mite showing the dorsal and ventral body setation (modified after Gutierrez, J. (1985), not to scale).

in Hoyer's medium. The females were mounted dorsal side-up so as to expose the dorso-central hysterosomal setae (D_1, D_2 and D_3) (Fig. 24; Plate, 6), while males were mounted in profile in order to facilitate the examination of the aedeagus (Plate, 7; Fig., 34).

The setae lengths, their inter-setal distances (D_1-D_2 and D_2-D_3) and the female's body length were measured under an M29 Wild Leitz phase contrast microscope. The weighted mean setae lengths (Tables, 16 and 17 and Figs., 25 and 26), were then classified according to the method developed by Rogo *et al.*, (1987) (Table, 1). The relationship between the lengths and their weighted mean inter-setal distances for the 6 founder females as well as the F_1 generation were recorded (Tables, 18 and 19; Fig., 27). In addition, the mean inter-setal distances for the F_1 generation was recorded (Table, 19) showing the extreme variation in setae lengths of 30 female specimens from each of the six sites. Body length measurements were also taken (Table, 23; Fig., 29) Correlation analysis was carried out between the setae lengths and their distances from each other using a SAS (Statistical Analysis System) software package (Tables, 24-26) in a bid to test whether the test populations fit the description of M.

tanajoa, *M. progresivus* or not. The ratio of the setae lengths and the inter-setal distances to the body length was also examined (Table, 24; Fig., 30; Appendices, 12-17) so as to determine the relationship between the change in setae length to any corresponding change in body length.

8.3 Results

The data presented (Tables, 16; Figs., 25) show that the founder females (n=6) as well as the resultant F_1 generation (n=180) (Table, 17; Fig., 26) had their setae lengths ranging from short to long in a continuum. In between this range, are found a category of intermediate setal forms. The range in weighted mean setae lengths varied from 20.02-45.76 µm among the founder females in all the six sites (Table, 16). Based on the length of their setae, the founder females from populations collected at Msambweni (South Coast) and Ithookwe (Kitui) were classified as long, while those from Rang'ala (Siaya) and Alupe (Busia) were classified as intermediate. Founder populations from Runyenje's (Embu) and Kamasengre (Rusinga island) populations were classified as short setaed (Table, 16; Fig., 25). When the setae of the inbred F_1 generation females were measured

Table 16. Weighted absolute dorso-central hysterosomal setae (D_1, D_2, D_3) lengths of founder females collected across 5 ecological zones in Kenya and used to establish 6 inbred F_1 CGM populations.

Ecological Zone	Founder line	Dorso-central hysterosomal setae measurements of founder mother (µm) (n=1)			Classification (Setal form)
		D_1	D_2	D_3	
I	Msambweni	31.46	40.04	45.76	Long
II	Kitui	22.88	28.60	42.90	Long
III	Embu	22.88	25.74	28.60	Short
IV	Rusinga	20.02	22.88	25.74	Short
IV	Busia	25.74	28.60	31.46	Intermediate
V	Siaya	25.74	28.60	37.18	Intermediate

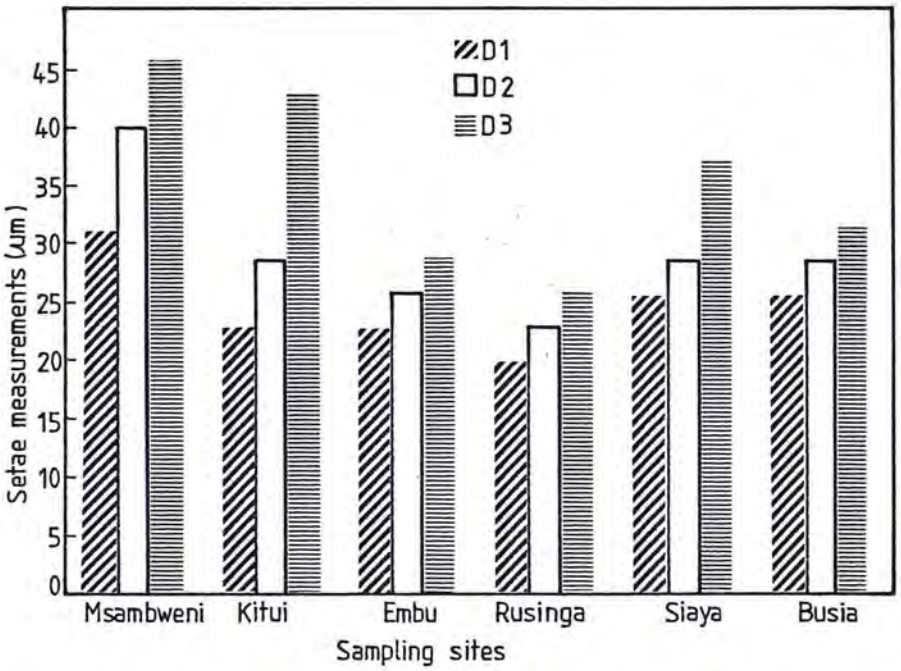

Fig. 25. Weighted mean dorso-central hysterosomal setae measurements of founder females among some CGM populations collected from six sites among five eco-climatic zones in Kenya.

Table 17. Weighted mean dorso-central hysterosomal setae (D_1, D_2, D_3) lengths of inbred F_1 generations collected from six sites in Kenya (n=30).

Ecological Zone	F_1 daughters	Dorso-central hysterosomal measurements of F_1 females (µm)						Classification (Setal form)
		D_1	S.E.	D_2	S.E.	D_3	S.E.	
I	Msambweni	22.25	±0.82	27.46	±1.02	33.24	±1.46	Long
II	Kitui	21.58	±0.53	25.59	±0.76	30.22	±0.76	Intermediate
III	Embu	19.88	±0.56	24.64	±1.13	30.60	±1.68	Intermediate
IV	Rusinga	18.49	±0.37	20.97	±0.36	25.74	±0.43	Short
IV	Busia	20.26	±0.67	25.45	±1.24	31.51	±1.62	Long
V	Siaya	17.56	±0.53	21.44	±0.76	26.19	±0.76	Short

Table 18. Weighted mean inter-setal distances (D_1-D_2, D_2-D_3) among founder females collected from six sites in Kenya (n=30)

Setae distance	Inter-setae distances (µm)					
	Msambweni	Kitui	Embu	Rusinga	Siaya	Busia
Distance 1 (D_1-D_2)	65.78	54.34	57.20	51.48	54.32	54.34
Distance 2 (D_2-D_3)	71.50	57.20	60.06	57.20	60.06	60.06

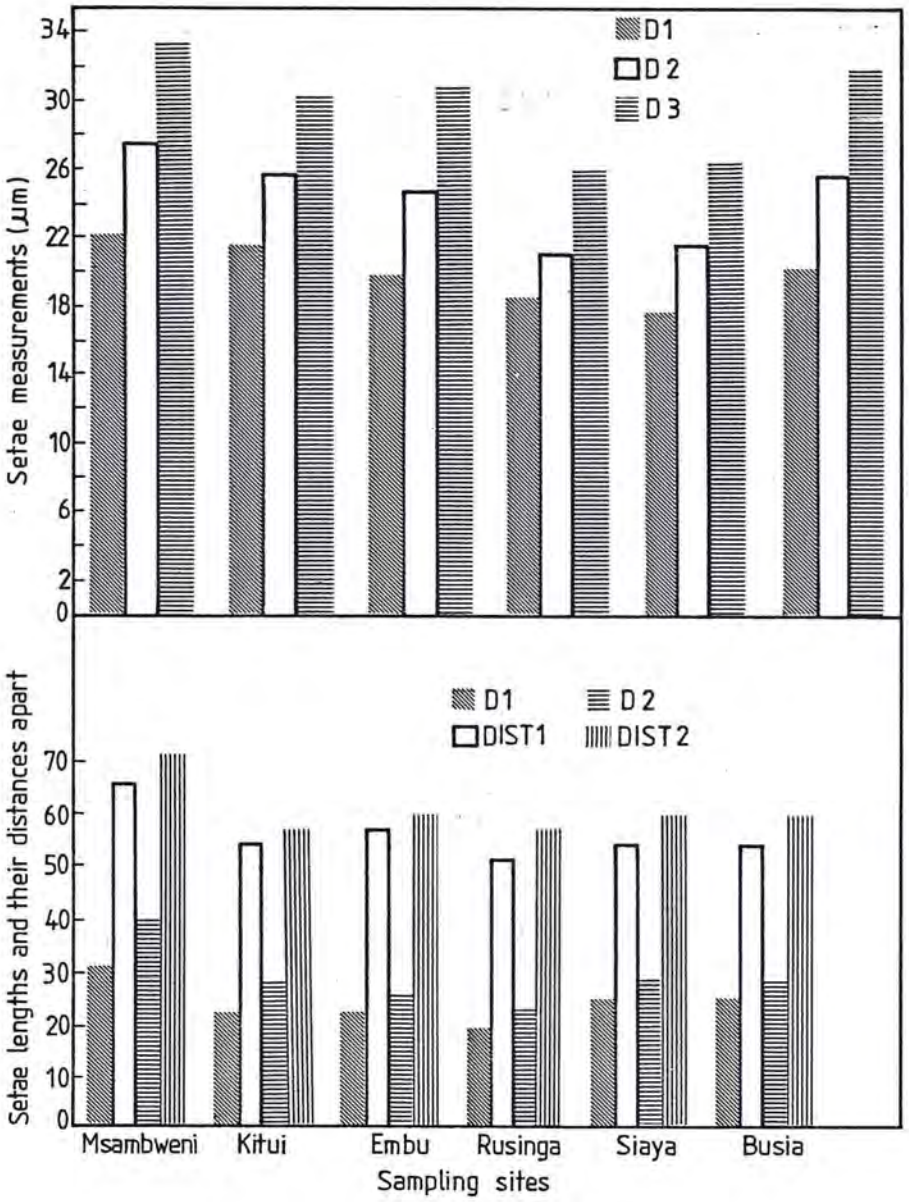

Fig. 26. Weighted mean dorso-central hysterosomal setae lengths (top graph) and their relationship with inter-setal distances (graph 2) of founder CGM females obtained from six sites among the five eco-climatic zones in Kenya.

Table 19. Weighted mean inter-setal distances (D_1-D_2, D_2-D_3) among some inbred F_1 generations collected from six sites in Kenya (n=30).

Sampling sites	Inter-setal distances (µm)	
	Distance 1 (D_1-D_2)	Distance 2 (D_2-D_3)
Msambweni	57.58 ±1.74	61.39 ±1.73
Kitui	53.39 ±0.99	56.25 ±0.89
Embu	54.33 ±1.31	59.29 ±1.17
Rusinga	54.43 ±0.87	58.82 ±0.96
Siaya	54.43 ±0.99	58.25 ±0.89
Busia	55.05 ±1.62	59.88 ±1.54

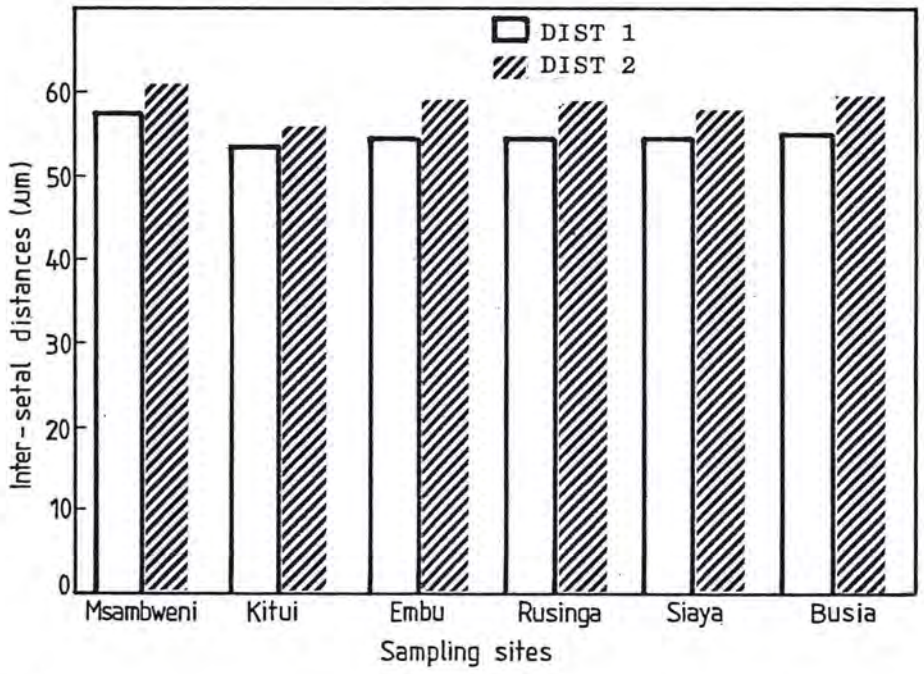

Fig. 27. Weighted mean inter-setal distances (D_1-D_2 and D_2-D_3) in an F_1 CGM generation obtained fron hybrid crosses of six founder females collected from among five eco-climatic zones in Kenya.

Table 20. The range of inter-setal distances (D_1-D_2, D_2-D_3) among some inbred F_1 generations from six sites in Kenya (n=30).

Site sampled	Range in inter-setae distances (µm)	
	Distance 1 (D_1-D_2)	Distance 2 (D_2-D_3)
	Range	Range
Msambweni	40.04-77.22	42.90-80.08
Kitui	37.18-68.64	40.04-71.50
Embu	42.90-71.50	48.62-77.22
Rusinga	42.90-65.78	48.62-71.50
Siaya	45.76-65.78	48.62-68.64
Busia	42.90-77.22	45.76-80.08

Table 21. Relationship between setae lengths (D_1, D_2) and their inter-setal distances(D_1-D_2, D_2-D_3) among founder females.

Ecological zone and sampling site	Setae and inter-setal distance measurements of founder parents (µm)			
	D_1	Dist1	D_2	Dist2
I Msambweni	31.46	65.78	40.04	71.50
II Kitui	22.88	54.34	28.60	57.20
III Embu	22.88	57.20	25.74	60.06
IV Busia	25.74	54.34	28.60	60.06
V Rusinga	20.02	51.48	22.88	57.20
V Siaya	25.74	54.32	28.60	60.06

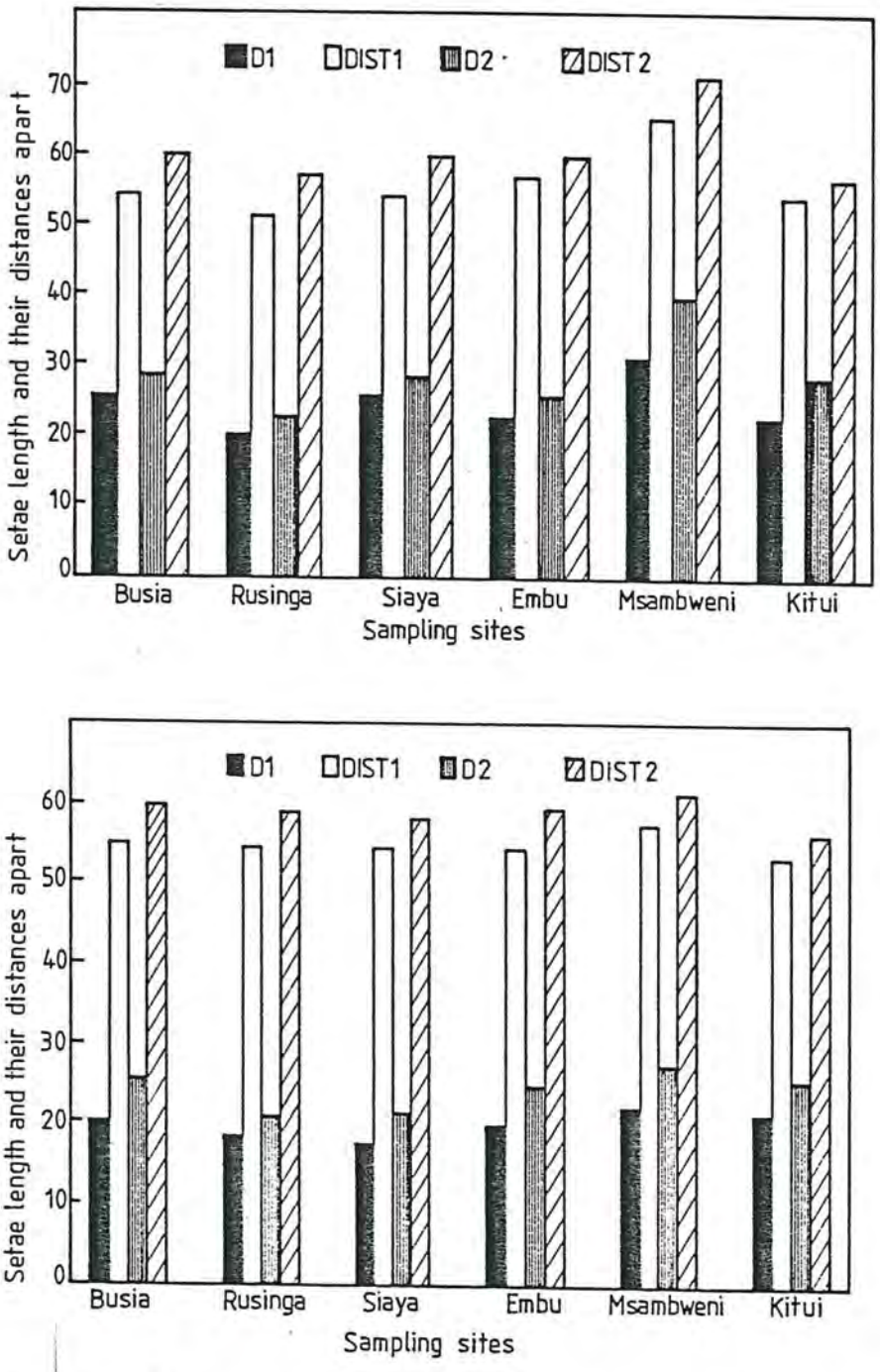

Fig. 28. Weighted mean dorso-central hysterosomal setae lengths (top graph) and their relationship with inter-setal distances (graph 2) of founder CGM females obtained from six sites among the five eco-climatic zones in Kenya.

Table 22. Relationship between setae lengths (D_1, D_2) and their inter-setal distances(D_1-D_2, D_2-D_3) among the F_1 generation (n=30).

Ecological zone and sampling site	Setae and inter-setal distance measurements of founder parents (µm)			
	D_1	Dist1	D_2	Dist2
I Msambweni	22.25 ±0.82	57.58 ±1.74	27.46 ±1.02	61.39 ±1.73
II Kitui	21.58 ±0.53	53.39 ±0.99	25.59 ±0.76	56.25 ±0.89
III Embu	19.88 ±0.56	54.33 ±1.31	24.64 ±1.13	59.29 ±1.17
IV Rusinga	18.49 ±0.37	54.43 ±0.87	20.97 ±0.36	58.82 ±0.96
IV Busia	20.26 ±0.67	55.05 ±1.62	25.45 ±1.24	59.88 ±1.54
V Siaya	17.56 ±0.53	54.43 ±0.99	21.44 ±0.76	58.25 ±0.89

Table 23. Variations between mean body lengths recorded among some CGM populations collected from six sites in Kenyan (n=30).

Collection site	Weighted mean body distance (µm)	S.E.	Range (µm)
Msambweni	430.52	± 5.81	352.80 - 482.16
Kitui	402.01	± 7.67	352.80 - 470.40
Embu	407.69	± 4.66	352.80 - 482.16
Rusinga	402.88	± 4.06	364.56 - 452.80
Siaya	402.19	± 4.06	352.80 - 458.64
Busia	410.84	± 7.66	352.80 - 482.16

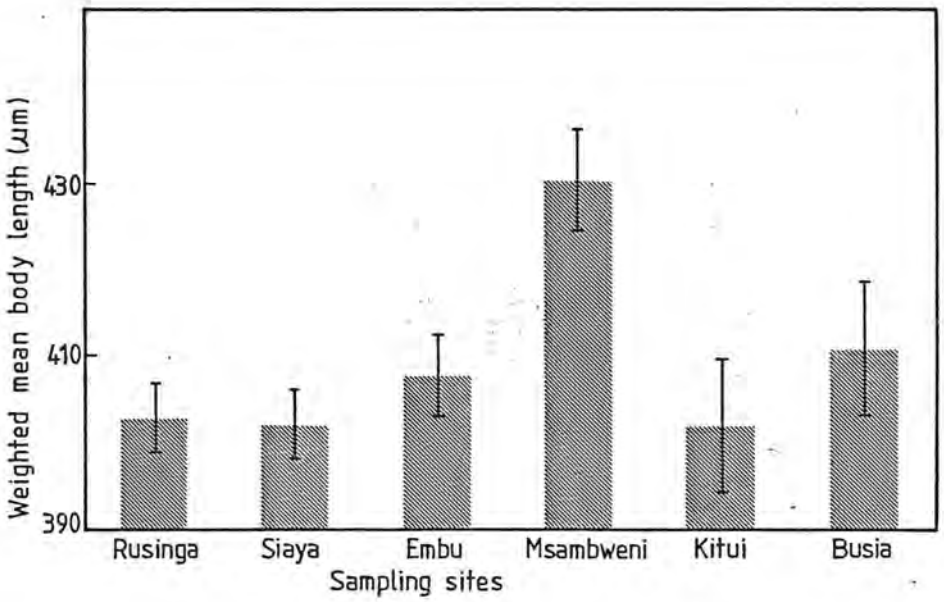

Fig. 29. Weighted mean body length of some CGM populations sampled from six sites among five eco-climatic zones in Kenya.

Table 24. Correlation analysis of the length of setae 1 [D_1] against inter-setal distances [D_1-D_2-D_3] and total body length of some CGM populations from Kenya (n=30; Ho: Rho=0).

Site	Distance 1 [D_1-D_2] (Corr.Coeff.)	p>|R|	Distance 2 [D_2-D_3] (Corr.Coeff.)	p>|R|	Total body length (Corr.Coeff.)	p>|R|
Msambweni	0.384	0.036	0.361	0.050	0.236	0.299
Kitui	0.614	0.0003	0.614	0.0003	0.596	0.0005
Embu	-0.272	0.145	- 0.151	0.425	0.052	0.783
Rusinga	-0.013	0.945	0.077	0.684	0.190	0.314
Siaya	-0.055	0.774	0.026	0.889	0.031	0.870
Busia	-0.154	0.416	-0.149	0.429	0.073	0.702

Table 25. Correlation analysis of the length of setae 2 [D_2] against inter-setal distances [D_1-D_2-D_3] and total body length of some CGM populations from Kenya (n=30; Ho: Rho=0).

	Distance 1		Distance 2		Body length	
Site	[D_1-D_2] (Corr.Coeff.)	p>|R|	[D_2-D_3] (Corr.Coeff.)	p>|R|	length (Corr.Coeff.)	p>|R|
Msambweni	0.528	0.003	0.525	0.003	0.402	0.028
Kitui	0.732	0.0001	0.733	0.0001	0.710	0.0001
Embu	-0.222	0.238	-0.107	0.572	0.053	0.780
Rusinga	0.134	0.481	0.112	0.554	0.298	0.109
Siaya	0.075	0.692	0.173	0.360	0.002	0.993
Busia	-0.088	0.645	-0.167	0.930	-0.011	0.955

Table 26. Correlation analysis of the length of setae 3 [D_3] against inter-setal distances [D_1-D_2-D_3] and total body length of some CGM populations from Kenya (n=30; Ho: Rho=0).

Site	Distance 1 [D_1-D_2] (Corr.Coeff.)	p>|R|	Distance 2 [D_2-D_3] (Corr.Coeff.)	p>|R|	Total body length (Corr.Coeff.)	p>|R|
Msambweni	0.619	0.0003	0.598	0.0005	0.540	0.002
Kitui	0.688	0.0001	0.688	0.0001	0.663	0.0001
Embu	-0.157	0.408	- 0.117	0.537	0.182	0.335
Rusinga	0.196	0.298	0.178	0.347	0.229	0.221
Siaya	0.058	0.761	0.070	0.712	0.036	0.848
Busia	-0.082	0.668	-0.033	0.861	0.030	0.874

Table 27. Relationship between the body length and CGM diagnostic parameters.

SAMPLE SITE	PARAMETER VALUES (RATIO OF THE BODY LENGTH)					
	D_1	D_2	D_3	$DIST_1$	$DIST_2$	MEAN SETAE LENGTH
MSAMBWENI	0.05195 a	0.06388 a	0.07697 a	0.13370 a	0.14251 a	0.06427 a
KITUI	0.05357 abc	0.06347 a	0.07472 ab	0.13214 a	0.13929 a	0.06392 a
EMBU	0.04900 a	0.06071 a	0.07517 ab	0.13345 a	0.14579 a	0.06163 a
RUSINGA	0.04599 bc	0.05213 b	0.06400 b	0.13509 a	0.14607 a	0.05404 b
SIAYA	0.04381 c	0.05352 b	0.06535 ab	0.13555 a	0.14510 a	0.06324 b
BUSIA	0.04974 ab	0.06259 a	0.07739 a	0.13540 a	0.14656 a	0.06324 a

Means with the same letter are not significantly different (Student-Neuman-Keuls test)

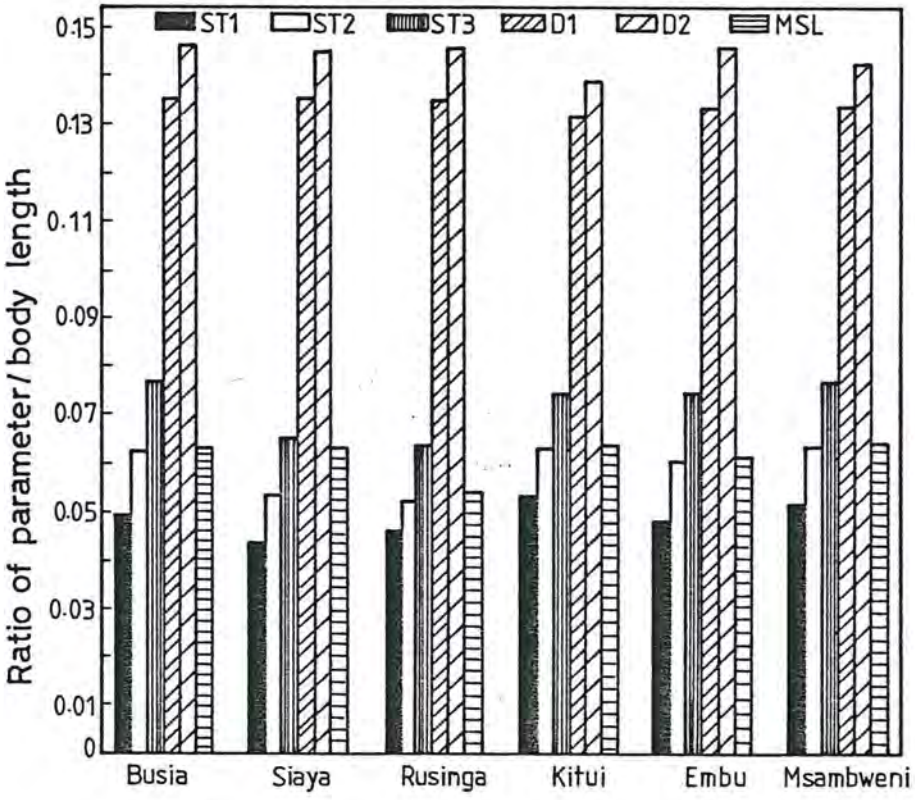

Fig. 30. The relationship between the ratio of dorso-central hysterosomal setae (D_1, D_2 and D_3), the mean inter-setal length ($D_1+D_2+D_3/3$) and their inter-setal distances (D_1-D_2 and D_2-D_3) to the mean body length of some CGM populations obtained from six sites among the five eco-climatic zones in Kenya(ST1=D_1, ST2=D_2, ST3=D_3, D1=distance1, D_2=distance2, MSL=mean setae length).

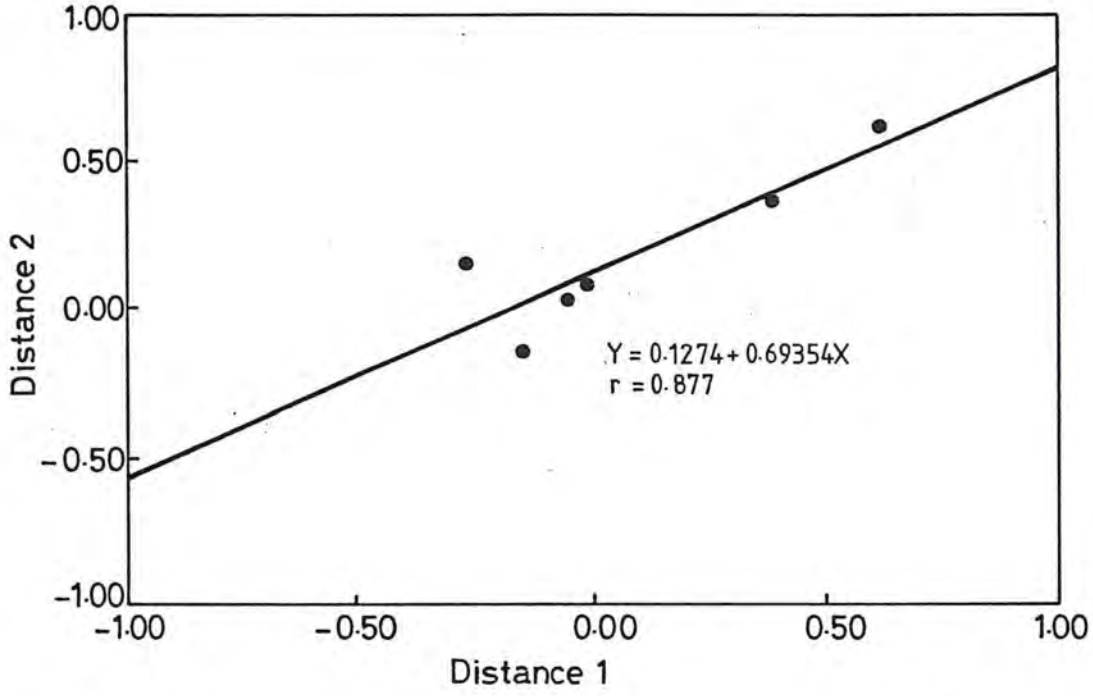

Fig. 31. Correlation analysis of the length of D_1 setae on inter-setal distances (D_1-D_2 and D_2-D_3).

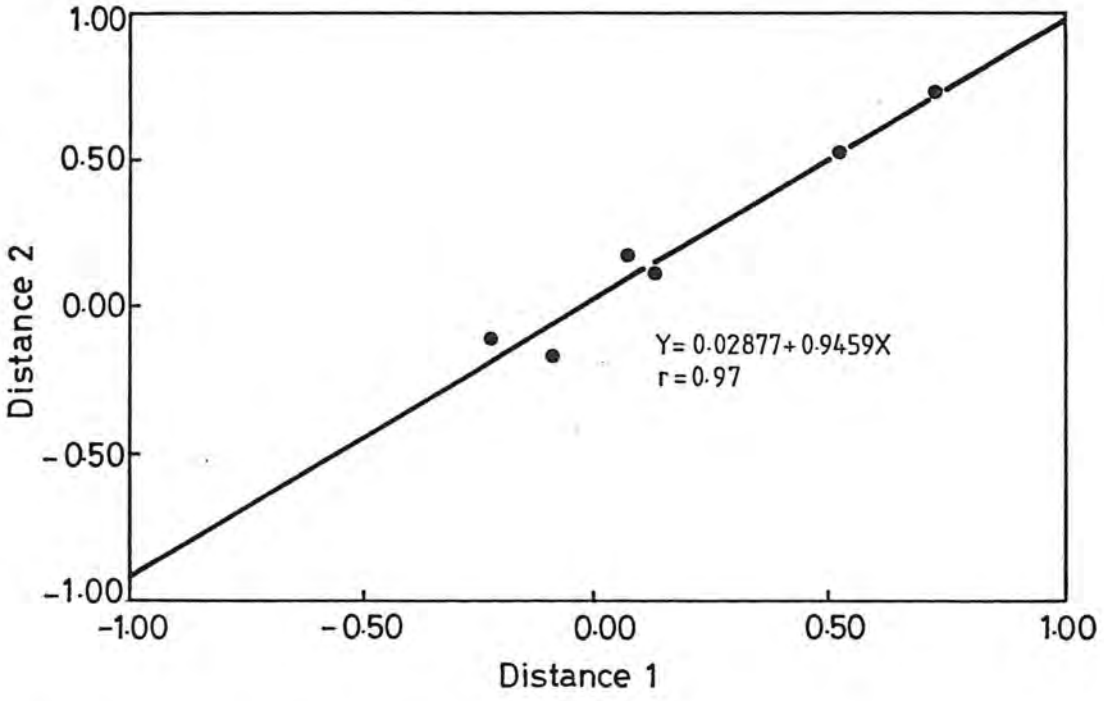

Fig. 32. Correlation analysis of the length of D_2 setae on inter-setal distances (D_1-D_2 and D_2-D_3).

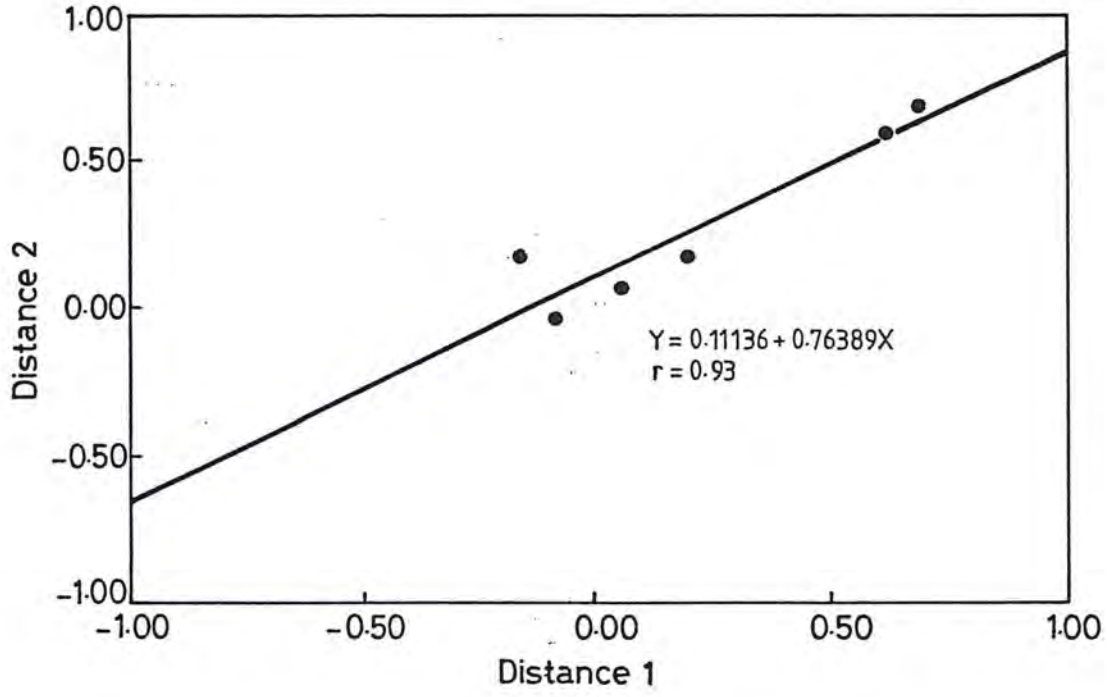

Fig. 33: Correlation analysis of the length of D_3 setae on inter-setal distances (D_1-D_2 and D_2-D_3).

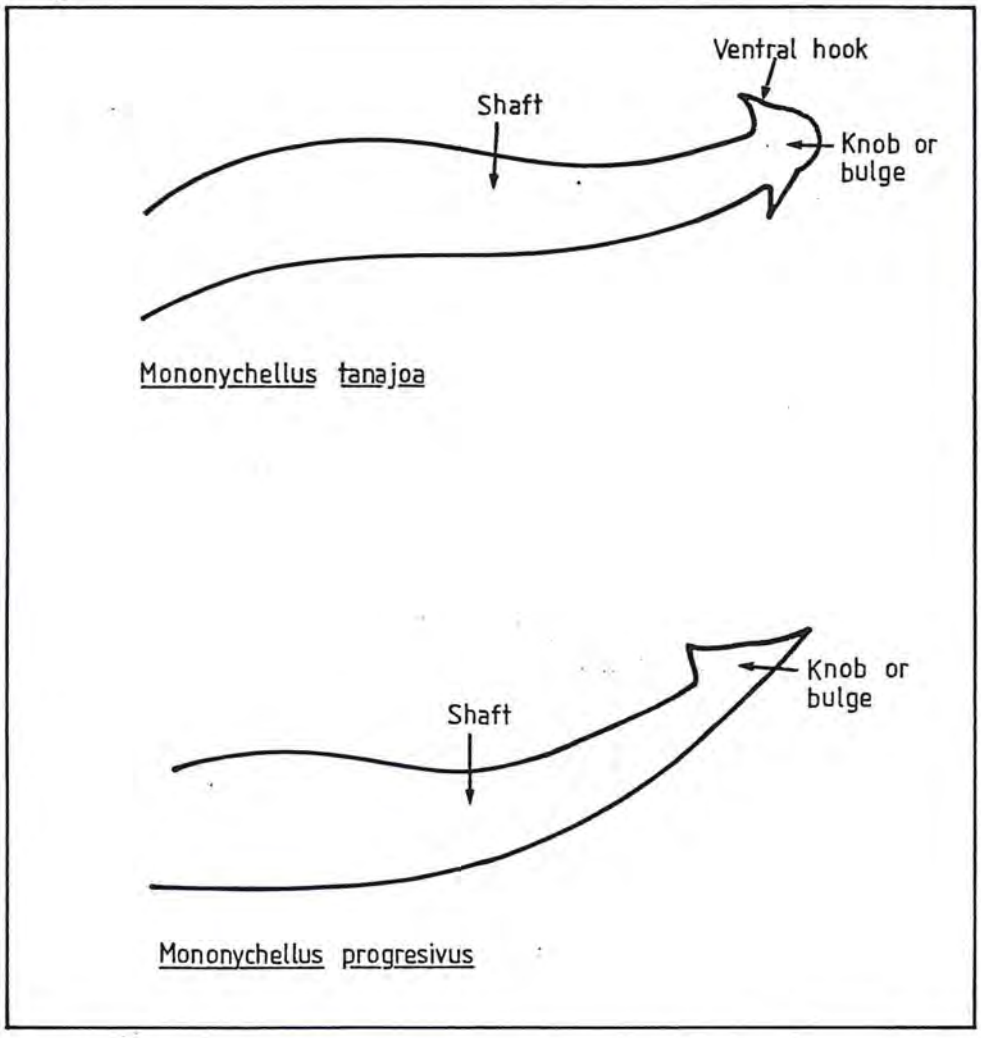

Fig. 34. Schematic representation ofthe male genital armature of *Mononychellus tanajoa* and *M. progresivus* (After Gutierrez, J. (1987) and MacFarlane, D. (1984), not to scale)

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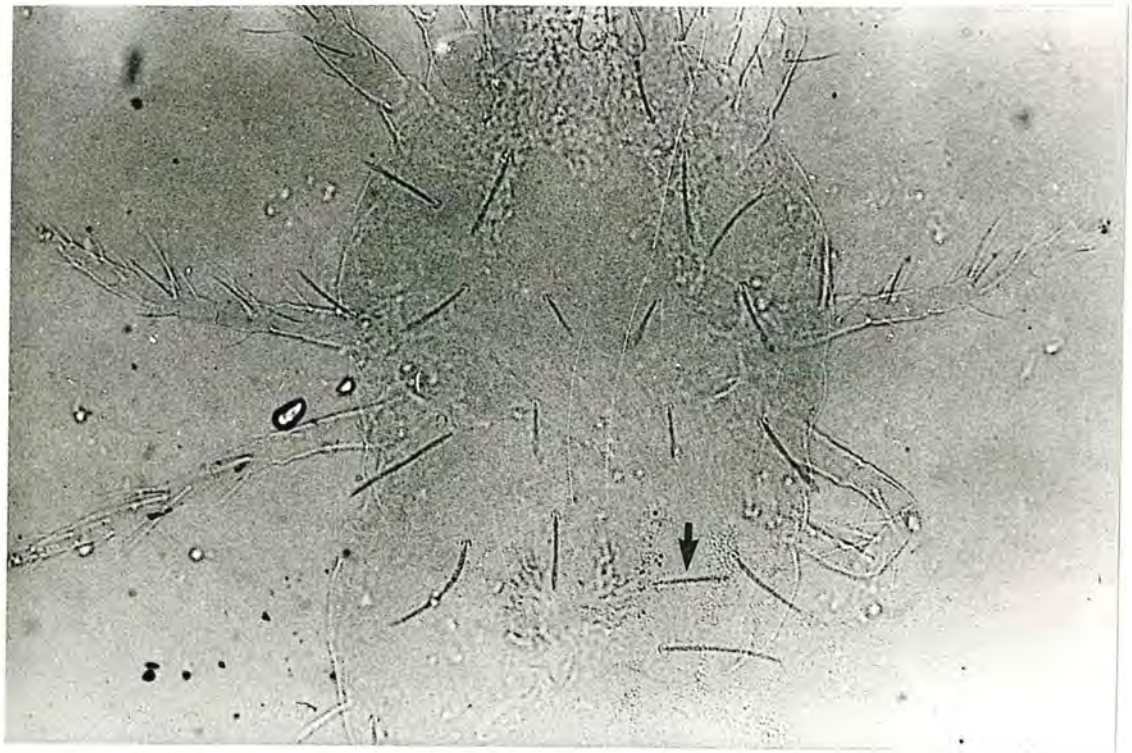

Plate 8. Displaced D_3 setae on the dorsum of a CGM female (arrow, X1000 times)

they were found to range from 17.56-33.24 µm (Table, 17; Fig. 26). In the classification of the F_1 females, the Msambweni (South Coast) and Alupe (Busia) populations were found to be long setaed but the Ithookwe (Kitui) and Runyenje's (Embu) were classified as intermediate forms. The F_1 daughters from Rang'ala (Siaya) and Kamasengre (Rusinga island) were found to be short setaed (Table, 17; Fig., 26). From one of the F_1 generation specimens, a unique phenomenon was observed whereby the D_3 setae on the right (Plate, 8), has shifted from its expected position thus making the task of species identification difficult.

It would be expected that setae inheritance is controlled by a single dominant gene, enabling the mites to inherit their parental setae characteristics in a simple Mendelian fashion but a close scrutiny of the data (Tables, 16 and 17; Fig., 25 and 26) shows that the setae segregate into three distinguishable phenotypes, the short, the intermediate and the long setaed forms. The above data, therefore, show that heterogeneity may exist in the populations examined because the three phenotypes arise from a single identifiable phenotype. Similar variations were observed in the measurements of inter-setal

distances (Tables, 18-22 and Fig., 26-28).

Overall, three relationships which combine the characteristics of *M. tanajoa* and *M. progresivus* can be distinguished: that the setae lengths are such that $D_3 > D_2 > D_1$ (Tables, 16, 17, 21, 22; Fig., 25, 26), that $Distance_2 > Distance_1$ such that the D_1 and D_2 setae are approximately $^1/_2$ as long as their respective inter-setal distances, D_1-D_2 (dist1) and D_2-D_3 (dist2) (Tables 18-22; Figs., 26, 27 and 28). The range in inter-setal distances (D_1-D_2 and D_2-D_3) of the F_1 generation varied from 37.18-80.08 µm (Table, 20). The great variability in these inter-setal distances is a pointer to their inherent instability as species diagnostic characters. The profiles of all the aedeagii examined were of the same shape suggesting the existence of only one species (Plate, 7; Fig. 34)

The body length measurements (Table, 23; Fig. 29) show that variation occurs in mites collected from the six sites (range 352-482 µm). Msambweni from the coast had the largest mites (mean=430 µm) (Fig., 29). Probably the hot humid coastal climate and luxuriant leaf growth has a role to play in the body size. There was poor correlation between the setae lengths and their respective distances from each other (Tables, 24-

26; Figs., 31-33), suggesting that these two parameters vary independently of each other and there is no detectable relationship between them that can be used to designate the CGM to the species level contrary to what was reported by MacFarlane (1984).

The ratio of setae lengths and their inter-setal distances in relation to the body length was also examined (Table, 24; Fig., 30) with the aim of finding out whether the setae lengths and hence their inter-setal distances increase with the corresponding increase in body length (Appendices, 12-17). For setae lengths it was found that an increase in body length is accompanied by a corresponding increase in setae length ($p<0.0035$; Appendices, 12-14). When the setae lengths (D_1, D_2 and D_3) were averaged and compared to the mean body length, they were found also to increase with a corresponding increase in body size ($p<0.0003$; Appendix, 17). However, the inter-setal distances remained constant and were not dependent on the increase in body length ($p>0.5$; Appendices, 15 and 16). The mean setae lengths were significantly different ($p<0.0003$; Appendix, 17) among all the six sites showing that although the mites were of a heterogeneous nature in setae composition they interbred (Table, 17).

The inter-setal distances (Table, 24) were not statistically different among the six sites tested. The plots of the relationship between setae lengths and their inter-setal distances with the varying body size are shown in Figs., 31-33. The correlation coefficients (r= 0.877, 0.97 and 0.93 for the D_1, D_2 and D_3 lengths, respectively), show a linear relationship between setae lengths and the body size in the manner described by Doreste (1981) for M. *progresivus* that $D_3 > D_2 > D_1$. Although the correlation coefficients show that inter-setal distances change with the corresponding setal lengths, the coefficients do not allow us to say by how much this change occurs. However, this information is readily available (Tables, 16 and 17, 21 and 22) which reveal that the setae lengths are $>1/2$ the inter-setal distances and thereby supporting the hypothesis that the populations handled probably belong to M. *progresivus* species.

8.4 Discussion

Flechtmann (1977), reported that setae may shift, drop or extra pairs added during development. This phenomenon is depicted in Plate 8 whereby the D3 setae from the right side has

either shifted or dropped off from its expected position. This evidence casts doubts on the reliability of setal characters for species categorization because of their great variability.

The mixed populations in the F_1 generation is evidence for the polygenic inheritance of the setae. Monroe (1963) attributed the inheritance of the carmine and the green colour forms in hybridized strains of *Tetranychus urticae* complex to a pair of two non-allelic genes. In the present studies, the three segregating phenotypes implies that the genotype consists of three pairs of non-allelic genes. Experiments to verify whether this polygenic mode of setae inheritance also applies among the subsequent F_2 and F_3 generations would further support the data presented in the current studies.

Sexual compatibility between members of different spider mites species is prevented in nature by the presence of a pre-zygotic mating barrier manifested as species-specific lock-and-key system between the male and the female genitalia (Gutierrez, 1987). *Mononychellus* has been shown to be arrhenotokous (chapter, 7). The genetic implication of this male haploidy is made clear if we examine the relationship between the two sexes during copulation. The Bryobinae

aedeagus is a simple sheath, but in the Tetranychinae the aedeagus as a rule is more complicated consisting of a shaft and a knob. The male's knob and the female's copulatory pore is a critical lock-and-key system (Gutierrez, 1985). Furthermore, the 6 populations were shown to hybridize as the single crosses resulted in a viable F_1 generation of uniparental and biparental F_1 sons and daughters respectively. Despite being allopatric, the 6 CCM populations collected from 5 diverse eco-climatic zones share a common gene pool and are, therefore, conspecific and thus of the same species. The shape of the aedeagus can be used for species identification. The shape of the male terminalia was not considered prior to 1968 when Livschitz and Croche discovered the male of *M. carribeanae* and again in 1981 when Doreste described the male of *M. progresivus*. This information is useful in identifying the mite precisely thereby facilitating the evisaged biocontrol measures.

It is interesting that the apparent segregation of the setal characters occurred on all the populations reared in the laboratory under the same conditions but which had been collected from different ecological zones which vary in altitude, temperature and geographical location.

Environmental stress which could result from such factors as poor food quality, unfavourable climate, competition, predation etc, may result in the remodelling of the mites genetic make-up in such a way that some unfavourable genotypes are suppressed in place of better fitted ones (Jesiotr et al., 1979).

This phenomenon is clearly exemplified by the data presented in Tables, 16 and 17; Figs., 25 and 26. It is shown that mites collected from Msambweni which has a hot and humid climate had particularly very long setae. The adaptive significance of these long setae is not very clear from the present studies.

Spider mites are web spinners. It is hypothesized that this may have a bearing on the significance of the inheritance of such long dorsal setae. Spider mites have evolved certain behavioural patterns in response to the webs they spin (Saito, 1985). The webs are used for protection against predators as they considerably reduce their searching efficieny. It is not clear how the Msambweni populations do not become hampered in their movement without getting entangled on the "roof" of the web on account of their long setae. Probably, the mites have overcome this by building a higher web "roof".

Whether this is the case or not, need to be investigated.

The available local predators have had little time to co-evolve with their prey in a bid to overcome this defensive mechanism. This is not surprising as the CGM being an exotic pest has no efficient local predators. The cassava tuber yield loss estimated to be as high as 80 % results from the feeding activities of these mites (Belloti and Bryne, 1979; Herren, 1987). The envisaged Africa-wide bilogical control programme of cassava pests using predators from the South American topotype is intended to fill this gap.

The measurements made on the dorso-central hysterosomals (D_1, D_2 and D_3) of the six selected populations consitute morphological characters that described M. tanajoa and M. *progresivus* which some workers supposedly ascribe distinct species status. These measurements answering to the description of M. *progresivus* are highly variable ranging from short-long in a continuum, among which lie forms having intermediate setal characteristics. Similar highly variable morphs were also reported by Rogo *et al.*, (1987). It is among these morphs that were shown to interbreed and which may account for the observed heterogeneity. It is clear, therefore,

why the intra-hybrid partial lethality (heterogeneity) is exhibited (chapter 6). This is because there exists polymorphic forms constituting the test populations.

From the data presented, it can be seen that no setae characteristic of *M. tanajoa* were detected. Aedeagii examination (Plate, 7 and Fig., 34), did not show the existence of the male species of *M. tanajoa*. Also, the setae measurements shown in Tables, 16-22 and Figs., 25-28, closely answer to the description of *M. progresivus*

The evidence deduced from the present studies show that fertilization took place among all the six populations as exemplified by the presence of diploid biparental daughters in the F_1 generation. This can only happen if the populations were of the same species as pre-mating mechanical barriers prevent copulation between members of different species. The formation of successful and viable hybrid zygotes means that the populations are conspecific and share the same gene pool. Sib-mating witnessed among spider mites from all the 19 test sites is a manifestation of the lock-and-key system between the male terminalium and the female's copulatory pore which ensures that gene exchange occurs only between

members of the same species.

9.0 SUMMARY

1. Inter-populational hybridization exposes the existence of inter-breeding populations which give rise to viable F_1, F_2 and F_3 progenies. Mortality is highest in the F_2 but lower in the F_1 and F_3, respectively ($F_1 < F_2 > F_3$).

2. Mortality in the reciprocal crosses differ from the test crosses implying that cytoplasmic factors are involved in the expression of the partial sterility.

3. This is not in agreement with Mendel's first law of inheritance and is further proof of the influence of cytoplasmic factors in the expression of partial hybrid sterility.

4. There is enhanced F_3 fertility or viability restoring effect as a result of mating of the progeny with males from the original parental line.

5. Genetic proof of the male origin is provided by sex inheritance studies which show that females are biparental and diploid while males are uniparental and haploid. Since

males are produced by arrhenotokous parthenogenesis, their genome is derived exclusively from their mothers while females inherit a complement of both paternal and maternal set of chromosomes.

6. Successful copulation, hybrid formation and the absence of complete hybrid sterility implied that pre- and post-zygotic inter-breeding barriers were absent and therefore the populations tested are phylogenetically the same as they share a common gene pool.

7. The partial lethality shown is a common feature in spider mites and occurs also among laboratory strains. Such a seemingly rapid adaptive divergence is under intense selection pressure and is facilitated by the short mean generation times and food availability.

8. The sub-specific differenes noted among populations from Central Kenya, further attests to the above observation. They could also be due to introgressive hybrid swarms resulting from introduction of genetically diverse populations from outside. This

diversity was expressed in the observed heterogeneity. However, these same populations were shown to share a common gene pool as they interbreed and are, therefore, not genetically different as indicated through Anova tests.

9. In intra-check crosses, the Anova tests showed that all the 19 CGM populations were not genetically different. Heterogeneity averaged 10% and could be due to the existence of the 3 setal morphs.

10 "Normal" sex-ratios were obtained, skewed sex-ratios in favour of males were not detected. This clearly shows that pre-zygotic isolation mechanisms were absent.

11. *M. tanajoa* males were not observed in this experiment but only *M. progresivus* males.

12. Male species is indicated by the species status of its mother, since it inherits half the chromosomal component from it and is, therefore, of the same species as its mother.

13. Males arise by arrhenotokous.

parthenogenesis.

14. Chaetotaxy studies reported during these investigations shows the existence of only one species with a gradient of complex morphs which show incomplete genetic divergence.

15. Populations from the hot and humid Msambweni had particularly long setae. The adaptive significance of these long setae is unkown and needs further investigation.

16. The setae were found to segregate into three identifiable phenotypes, the long, the short and the intermediate setal forms.

17. The mode of inheritance of the setae may be polygenic and is controlled by a pair of three non-allelic genes.

18. The setae patterns detected resembled *M. progresivus*, no *M. tanjoa* was seen.

19. Setae length was found to be correlated with body size.

20. The male genital armature was found to be

the more genetically stable species diagnostic tool than dorso-central hysterosomal setae lengths and their inter-setal distances.

21. The results presented in this study were on populations from Kenya. There is need to diversify this work to cover the rest of Africa especially West Africa from whose specimens Flechtmann described the first incidence of *M. progresivus* Doreste, from Nigeria and Gabon in 1982. The strict requirements for sanitary certificates, curtailed genetic isolation studies among CGM populations from the rest of the African countries as this involves use of live material.

10.0 CONCLUSION

Synthesis of all the information generated in this study suggest that the CGM populations tested belong to the species *M. progresivus* Doreste 1981. It is possible that the first CGM species reported from Uganda as *M. tanajoa*, may have been misidentified as this was based on female setae characters. It is thus concluded that the different populations handled represent segments of the same species and that the species names *M. tanajoa* (Bondar, 1938), Flechtmann and Baker, 1970 and *M. progresivus* Doreste, 1981 refer to the same species

The clarification of the exact identity of the CGM now gives the biocontrol experts of the Africa Wide Biological Control Programme for Cassava Pests, the impetus to explore for the natural enemies of the mite in the original South American habitat especially Venezuela from where the CGM introduced into Africa was described by Doreste in 1981 as *M. progresivus*.

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Appendix 1. Anova table for interpopulational hybrid crosses of some CGM populations from eco-climatic zones of Nyanza and Western Kenya.

Source	Df	Ss	Ss	F	P>F
Model	50	109.00282	2.18006	2.99	0.0001
Error	141	102.92934	0.72999		
Corrected Total	191	21.93216			
		CV=42.62809			
Egg waves	3	3.08106	1.10270	1.41	0.2433
Filgen	2	42.16356	21.08178	28.88	0.0001
Site	15	33.89953	2.08178	3.10	0.0002
Site* Filgen	30	29.85863	0.99528	1.36	0.1182

Snk grouping for filial generations

A	1.419	F1
B	2.567	F2
C	2.027	F3

Appendix 2. Anova table for reciprocal crosses of some CGM populations from eco-climatic zones of Nyanza and Western Kenya.

Source	Df	Ss	Ss	F	P>F
Model	47	104.00765	2.21293	2.97	0.0001
Error	132	98.37919	0.74529		
Corrected Total	179	202.38683			
		CV=43.23664			
Egg waves	3	3.46170	1.15472	1.55	0.2048
Filgen	2	37.74712	18.87356	25.32	0.0001
Site	14	33.73288	2.40949	3.23	0.0002
Site* Filgen	28	29.06347	1.03798	1.39	0.1103

Snk grouping for filial generations

A	1.434	F1
B	2.555	F2
C	2.001	F3

Appendix 3. Anova table for inter-populational hybrid crosses of some CGM populations from the eco-climatic zones of Eastern and Central Kenya.

Source	Df	Ss	Ss	F	P>F
Model	86	798.53	9.28	2.35	0.0001
Error	249	966.79	3.88		
Corrected Total	335	1765.33			
		CV=24.98			
Egg waves	3	135.02	45.01	11.59	0.0001
Filgen	2	115.76	57.88	14.91	0.0001
Site	27	108.17	4.01	1.03	0.4261
Site* Filgen	54	439.59	8.14	8.14	0.0001

Snk grouping for generation group means

A	7.901	F_1
B	8.477	F_2
C	6.087	F_3

Appendix 4. Anova table for reciprocal crosses of some CGM populations from the eco-climatic zones of the Eastern and Central Kenya.

Source	df	ss	Ms	F	P>F
Model	39	688.21	7.73	1.48	0.0096
Error	258	1349.18	5.23		
Corrected total	347	2037.39			
		CV=29.45			
Filial generations	2	88.52	44.26	8.46	0.0003
Sites	27	167.22	5.97	1.14	0.2896
Egg waves	3	22.71	7.57	1.45	0.2294
Filial generations* Sites	54	409.76	7.32	1.40	0.0436

Snk grouping for filial generations

A	7.121	F1
B	8.35	F2
C	6.83	F3

Appendix 5: Anova table for inter-populational hybrid crosses of some CGM populations from eco-climatic zone of the Coast.

Source	df	ss	Ms	F	P>F
Model	20	36.64	1.83	6.91	0.0039
Error	51	13.53	0.26		
Corrected total	71	50.17			
		CV=26.08			
Filial generations	2	30.26	15.13	57.03	0.0001
Site	5	0.72	0.14	0.54	0.7430
Egg waves	3	4.01	1.34	5.04	0.0039
Filial generations* Site	10	1.64	0.16	0.62	0.7900

Snk grouping for filial generations

A	1.95	F1
B	2.78	F2
C	1.19	F3

Appendix 6. Anova table for reciprocal crosses of some CGM populations from the eco-climatic zone of the Coast.

Source	df	ss	Ms	F	P>F
Model	20	24.69	1.23	5.33	0.0001
Error	51	11.81	0.23		
Corrected total	71	36.50			
		CV=22.57			
Egg waves	3	3.01	1.00	4.33	0.0085
Filial generations	2	19.27	9.63	41.61	0.0001
Site	5	0.91	0.18	0.79	0.5624
Filial generations* sites	10	1.51	0.15	0.65	0.7637

Snk grouping for filial generations

A	2.09	F1
B	2.78	F2
C	1.52	F3

Appendix 7. Anova table for inter-populational hybrid crosses of some CGM populations from Coastal and up-country eco-climatic zones of Kenya.

Source	Df	Ss	Ss	F	P>F
Model	38	48.12	1.27	2.32	0.0004
Error	105	57.25	0.55		
Corrected Total	143	105.37			
		CV=36.15			
Egg waves	3	7.07	2.361	4.33	0.0064
Filgen	2	31.60	15.80	28.98	0.0001
Site	10	5.40	0.49	0.90	0.5426
Site* Filgen	20	4.04	0.18	0.34	0.9976

Snk grouping for generation group means

A	2.61	F_2
B	2.06	F_1
C	1.45	F_3

Appendix 8. Anova table for reciprocal crosses of some CGM populations from the eco-climatic zones of the Coast and up-country

Source	df	ss	Ms	F	P>F
Model	38	47.60	1.25	2.83	0.0001
Error	105	46.42	0.44		
Corrected total	143	94.02			
		CV=31.84			
Egg waves	3	2.27	0.76	1.71	0.1694
Filial generations	2	38.87	19.43	43.96	0.0001
Sites	10	3.52	0.32	0.72	0.71
Filial generations* Sites	20	2.94	0.13	0.30	0.9989

Snk grouping for filial generations

A	2.11	F1
B	2.71	F2
C	1.44	F3

Appendix 9:Anova table for intra-populational check crosses of some CGM populations from Nyanza and Western Kenya.

Source	Df	Ss	Ss	F	P>F
Model	20	67.06583	3.35329	4.71	0.0001
Error	51	36.31513	0.71206		
Corrected Total	71	103.38095			
		CV=41.18378			
Egg waves	3	0.50264	0.16755	0.24	0.8714
Filgen	2	31.75222	15.87611	22.30	0.0001
Site	5	20.69576	4.13915	5.81	0.0003
Site* Filgen	10	14.11519	1.41152	1.98	0.0550

Snk grouping for generation group means

A	1.140	G1
B	2.709	G2
C	2.298	G3

Appendix 10. Anova table for intra-populational check crosses of some CGM populations from Eastern and Central eco-climatic zones of Kenya.

Source	Df	Ss	Ss	F	P>F
Model	23	25.41	1.10	1.58	0.0727
Error	72	50.25	0.70		
Corrected Total	95	75.66			
		CV=48.56			
Egg waves	3	4.08	2.05	3.56	0.0094
Filgen	2	11.44	5.72	8.19	0.0006
Site	6	3.78	0.54	0.77	0.6114
Site* Filgen	12	10.19	0.73	1.04	0.4229

Snk grouping for generation group means

B	1.36	G_1
A	1.88	G_2
B	1.04	G_3

Appendix 11. Anova table for intra-populational check crosses of some CGM populations from Coastal eco-climatic zone.

Source	df	ss	Ms	F	P>F
Model	14	17.52	1.25	2.32	0.0023
Error	33	12.46	0.38		
Corrected total	47	29.98			

CV=29.85

Egg waves	3	2.66	0.89	2.35	0.0900
Filial generations	2	13.90	6.95	18.41	0.0001
Sites	3	0.30	0.100	0.27	0.8495
Filial generations* Sites	6	0.66	0.11	0.29	0.9357

Snk grouping for mean group generations

A	3.70	G1
B	5.77	G2
C	2.90	G3

Appendix 12. Relationship between the ratio of the D_1 setae to the total body length of some CGM populations collected from six sites among the five eco-climatic zones of Kenya.

Source	Df	Ss	Ss	F	P>F
Model	5	0.00198	0.00039	5.40	0.0004
Error	174	0.012180	0.00007		
Corrected Total	179	0.01478			
		CV=17.50167			
Site	5	0.00198	0.00039	5.40	0.0001

Appendix 13. Relationship between the ratio of the D_2 setae to the total body length of some CGM populations collected from six sites among the five eco-climatic zones of Kenya.

Source	Df	Ss	Ss	F	P>F
Model	5	0.00408	0.00081	5.11	0.0002
Error	174	0.02776	0.00016		
Corrected Total	179	0.03184			
		CV=21.27311			
Site	5	0.00408	0.00081	5.11	0.0002

Appendix 14. Relationship between the ratio of the D_3 setae to the total body length of some CGM populations collected from six sites among the five eco-climatic zones of Kenya.

Source	Df	Ss	Ss	F	P>F
Model	5	0.00537	0.00107	3.67	0.0035
Error	174	0.05094	0.00029		
Corrected Total	179	0.05632			
		CV=23.67755			
Site	5	0.00537	0.00107	3.67	0.0035

Appendix 15. Relationship between the ratio of distancel (D_1-D_2) to the total body length of some CGM populations collected from six sites among the five eco-climatic zones of Kenya.

Source	Df	Ss	Ss	F	P>F
Model	5	0.00027	0.00005	0.19	0.9657
Error	174	0.04988	0.00028		
Corrected Total	179	0.05015			
		CV=12.61432			
Site	5	0.00027	0.00005	0.19	0.9657

Appendix 16. Relationship between the ratio of distance2 (D_2-D_3) to the total body length of some CGM populations collected from six sites among the five eco-climatic zones of Kenya.

Source	Df	Ss	Ss	F	P>F
Model	5	0.00118	0.00024	0.87	0.5024
Error	174	0.04720	0.00027		
Corrected Total	179	0.04838			
		CV=11.42031			
Site	5	0.00118	0.00024	0.87	0.5024

Appendix 17. Relationship between the ratio of the mean setae length to the total body length of some CGM populations collected from six sites among the five eco-climatic zones of Kenya.

Source	Df	Ss	Ss	F	P>F
Model	5	0.00346	0.00069	4.94	0.0003
Error	174	0.02436	0.00014		
Corrected Total	179	0.02783			
		CV=11.42031			
Site	5	0.00346	0.00069	4.94	0.0003