The structure of ant communities and their impact on soil-pupating pests in citrus orchards in the Grahamstown area of the Eastern Cape

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Abstract

Two ant species, *Pheidole megacephala* (Fabricius) and *Anoplolepis custodiens* (Smith) reach pest status in citrus orchards through precipitating outbreaks of homopterous pests. However, predacious ants, including these two ant species, play an important role in pest suppression in agroecosystems and are therefore beneficial to these systems. If *A. custodiens* and *P. megacephala* are important natural control agents in citrus, using ant bands to break the mutualism between the ants and the Homoptera as a method of ant control is preferable to poisoning. Ant communities were sampled by pitfall trapping in three experimental subunits of 2-, 4-, 15- and 30-year-old citrus orchards, in the Grahamstown area of the Eastern Cape. In one subunit in each orchard, populations of *P. megacephala* and *A. custodiens* were suppressed by poison applications. In a second subunit, trees were banded with trunk barriers so that ants were prevented from foraging in the trees and a third subunit served as the untreated control. Bait pupae of bollworm, false codling moth and fruit fly were planted in bait trays in all of the subunits to investigate predation on these citrus pests in the relative absence of predacious ants and where they were excluded from the trees. *Pheidole megacephala* dominated exclusively in all of the plots. Community composition did not change dramatically with increasing age of the trees, but species diversity and species abundance did. Rank-abundance curves showed that community diversity was highest in the 2-year-old plots and lowest in the 30-year-old plots. The Simpson and Shannon-Wiener diversity indices and their evenness measures indicated that diversity and equitability were highest in the poisoned subunits and lowest in the banded subunits. Principle component analysis revealed that the poisoned subunits were similar and distinct in species composition, that there was significant monthly variation in species composition and that community stability increases with an increase in orchard age. The presence of *P. megacephala* was significantly negatively correlated ($r_s = -0.293$; $p < 0.001$) with pest pupal survival. Pupal survival was significantly higher for bollworm ($p < 0.001$), FCM ($p < 0.001$) and fruit fly ($p < 0.001$) in the poisoned subunits, than in the banded and control subunits. There was a general trend for survivorship to increase with an increase in the age of the trees. A significant difference ($p < 0.001$) was found between the months in which the trials were carried out. Pupal survival was significantly lower ($p < 0.001$) for FCM than for bollworm and fruit fly. In citrus orchards, ant communities are organised by ecological processes and interactions and are influenced by methods of ant control. Ant bands are preferable to poisoning as a method of ant control, so that beneficial species are left on the ground to prey on pests that pupate in the soil. Maintaining high ant species diversity in citrus orchards would be beneficial as predation on the pupae was more effective where ant species diversity was higher.

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Preface

The author would like readers to note that Chapter 2 and Chapter 3 have been written up as scientific manuscripts and there is thus a fair amount of repetition, particularly in the Material and Methods sections, throughout the thesis.

1

Introduction

Summary

The history of citrus pest control in South Africa and the pest status of ants in citrus orchards are reviewed. A review of the literature on the benefits of predatory ants in agricultural systems is given. The aims and scope of the project and the biology of the economically important ant and pest species are outlined. A short description of the study site and the experimental orchards are given.

1.1 General introduction

In recent years, there has been an increasing focus on citrus entomology in agricultural research as the vast array of beneficial insects associated with citrus have posed the potential for a more natural approach to pest control and, as the monetary value of the annual crop has increased with the development and expansion of the overseas market for the fruit (Annecke & Moran, 1982).

The citrus industry in southern Africa produces an export revenue of approximately R1 500 million per annum (Bedford, 1998a) which represents a valuable contribution to the agricultural income of the countries in this region. The exported fruit represents 60% of total production, but accounts for 90% of total industry revenue (Bedford, 1998a). Thus the incentive for citrus growers to achieve the standards of quality required for export fruit is very high and pests are an obstacle in this respect (Annecke & Moran, 1982). The pest complex on citrus is large and, because even cosmetic damage is a culling factor for export fruit (Hofmeyer *et al.*, 1992), effective pest management and control in citrus orchards is vital.

To the economic entomologist, the term control means the existence of a condition where the population of an injurious insect is below the numerical level at which it begins to cause measurable economic damage (Thompson, 1956) or the limitation of insect numbers to density levels which are not significantly injurious to man’s material interests (Milne, 1957).

Until recently, pest control in agriculture has relied heavily on the use of insecticides. The most “effective” chemicals found for the identified pests were applied with little concern for other important factors in the agroecosystem (Pedigo, 2002). This kind of approach, where chemical pesticides were used without any regard for the complexities of the environment, caused major disruptions to the ecosystems to which they were applied (Smith & van den Bosch, 1967). Target pest species developed resistance to pesticides and could no longer be controlled effectively with chemicals (Smith & van den Bosch, 1967). Pesticides disrupted favourable natural enemy-pest balances which resulted in pest outbreaks. A ‘pest upset’ was the result of a pesticide being ineffective against a particular pest, destroying the pest’s normally effective natural enemies, thus allowing it to rise to new and higher levels. Pest resurgences resulted from the rapid recovery of a pest population that was initially suppressed by a pesticide that also destroyed that pest's natural enemies (Bartlett, 1964). The creation of new pests of species that were formerly harmless rarities resulted from the use of pesticides (De Bach, 1974). In addition to this, chemical pesticides and their residues may remain in or on the crop, and may drift to streams and drainages or to other crop areas, causing a health risk to man. Pesticides may also be detrimental to non-target species in the system such as pollinators and other beneficial organisms (Smith & van den Bosch, 1967; Pedigo, 2002). Clearly, the situation had to be reviewed.

As a result of the disruptions and problems caused by the purely insecticide-based approach to pest control, the development of biological control was encouraged, which emphasized the significant impact of effective natural enemies on pest populations (Pedigo, 2002). Biological control, stated as an entomological practice is "the study and utilization of parasites, predators and pathogens for the regulation of population densities of pests" (Doutt, 1967). However, for many pests, control by natural enemies alone is not effective. Consequently, the concept of integrated control was developed (Pedigo, 2002). Bartlett (1964) explained the term integrated control as follows: "By combining the advantageous features of both chemical and biological control, i.e., reducing the pests while causing minimum disruption to natural enemy activity, a greater permanence of pest suppression may be obtained. Treatments so designed have been termed complementary or integrated control programs". The integrated pest management approach advocates the combined use of control methods (both biological and chemical), and is based on a sound knowledge of the ecology of pest species and the agroecosystem (Smith & van den Bosch, 1967).

The role of biological control in pest suppression is an increasingly important aspect of an ecological approach to pest control. Biological control agents can be utilized and manipulated by man to enhance or favourably change the existing degree of biological control of a pest (De Bach, 1964). The use of predators as biological control agents in agriculture is increasing in emphasis, based on modern investigations and experiments. A significant feature to the development of integrated pest management programs has been the efficiency of predators in agroecosystems (Hagen *et al.*, 1976).

Pest control programs are now based largely on ecological principles. The three important elements of pest management are the use of multiple tactics (such as natural control agents, resistant varieties of crops and pesticides) in a compatible manner, the maintenance of pest populations below the levels at which they cause economic damage and conservation of the environment quality (Pedigo, 2002).

Pest management in South African citrus has experienced many of the problems characterized by incessant pesticide application. In the early days of citriculture and before the advent of parathion, pest control relied heavily on the fumigation of citrus trees with the toxic gas hydrogen cyanide (HCN) (Annecke, 1969; Annecke & Moran, 1982; Bedford, 1998b). With the introduction of parathion into South African citrus orchards in 1948 came a period of almost total reliance on chemical control until its detrimental effects on natural enemies (Annecke & Moran, 1982) lead to pest resurgences and the creation of completely new pest problems (Catling, 1971; Annecke & Moran, 1982). Infestations of California red scale, *Aonidiella aurantii* Maskell (Hemiptera: Diaspididae), one of the major citrus pests worldwide (including South Africa) became more serious (Bedford, 1968) and the status of pests such as soft brown scale, *Coccus hesperidum* L. (Hemiptera: Coccidae) and citrus red mite, *Panonychus citri* McGregor (Acari: Tetranychidae) increased as a result of parathion sprays (Annecke, 1959; 1969). This stimulated the use of mixtures and new formulations of insecticides, which were applied more frequently and at increasing concentrations until pesticide use became costly and further pest repercussions resulted (Annecke, 1969). An improvement in the situation resulted from a number of factors, including pest surveys, to determine the need for treatment, and consequently a reduced number of applications in a season and improvements in application and timing of pesticide treatments (Annecke, 1969).

In 1975, commercial citrus farmers were faced with the problem of the development of resistance of red scale to parathion (Georgala, 1975; Nel *et al.*, 1979). Coupled with this, the realisation that pesticide-induced outbreaks should be avoided, led growers to strive towards an integrated pest management (IPM) approach (Bedford, 1998b). An IPM approach is now widely used by South African commercial citrus farmers in which safe and selective pesticides are used together with indigenous or exotic natural enemies to achieve an adequate level of pest control (Annecke, 1969). An IPM approach to pest control in citrus consists of the integration of classical, conservation and augmentation biological control. The efficacy of the biological control agents then determines the extent of chemical control required for the maintenance of quality produce (Hattingh, 1994). The pesticides used in conjunction with an IPM approach should cause no repercussions or only mild repercussions (Bedford, 1998b) and although the activities of natural enemies do not eradicate pests, in many cases they are able to suppress pest populations to a level where they do not cause economic damage (Hofmeyer *et al.*, 1992).

An essential factor in the success of IPM programmes, particularly in terms of the biological control of red scale and other scale pests, is the control of ants (Hymenoptera: Formicidae) in citrus trees (DeBach *et al.*, 1951a; Annecke, 1963; Bedford, 1968). Ants are a major component of the citrus orchard fauna (Samways *et al.*, 1982) and indirectly they have serious negative effects on citrus through their mutualistic association with homopterous pests such as aphids, soft scales and mealybugs (Ullyett, 1938; Flanders, 1945; Annecke, 1958). The ants collect honeydew produced by these homopterans and in return, provide them with protection from their natural enemies - predators, parasitoids and even pathogens (Way, 1963; Samways, 1983a). This leads to a population increase of both mutualists (Annecke, 1959; De Bach *et al.*, 1951b) with serious economic consequences, as natural control agents are prevented from maintaining pest populations at commercially acceptable levels. Outbreaks or epidemics of other serious pests, particularly red scale, are an indirect result of this breakdown in natural control (Steyn, 1954a, b; Bedford, 1968). For biological control agents to be effective in suppressing pest populations, ant control is essential.

Two ant species in particular, the brown house ant, *Pheidole megacephala* (Fabricius), and the pugnacious ant, *Anoplolepis custodiens* (Smith), which are both abundant and widespread in South African citrus production areas, have serious negative effects on citrus and are by far the most economically important local ants (Samways *et al.*, 1982; 1998). Current management strategies for these ants include poisons (such as soil applications of insecticides) and the use of ant bands, which act as a physical barrier, preventing ants from entering the trees (Samways *et al.*, 1998).

However, predatory ants (including *A. custodiens* and *P. megacephala*) are known to have beneficial effects in agroecosystems. Ants utilize a wide variety of arthropods as nutrient sources (Gotwald, 1986) and direct behavioural observations and research studies have shown them to be important predators of agricultural pests. For example, Risch and Carroll (1982a, b) found that the pest problems caused by the ant, S*olenopsis geminata* Forel (Hymenoptera: Formicidae) in Mexican maize, squash and bean fields were outweighed by its beneficial effects in keeping insect numbers down. Although *P. megacephala* attacks insects beneficial to the crop and tends homopterous pests, its economic effect in Hawaiian pineapple is rated as positive (Phillips, 1934 *cited in* Gotwald, 1986). Coconut production in Tanzania benefitted from the presence of predatory ants, particularly *A. custodiens* (Löhr, 1992). Among the soil predators that attack fruit flies of the family Tephritidae (Diptera), ants are the most important. The life stages associated with the soil such as the mature larvae, pupae and newly emerged adults are the most susceptible to predation by ants (Bateman, 1972). Heavy mortality is inflicted by the Argentine ant, *Linepithema humile* Mayr (Hymenoptera: Formicidae) on pupae of the Mediterranean fruit fly, *Ceratitis capitata* Wiedemann (Diptera: Tephritidae) in the soil beneath fruit trees in Hawaii (Wong *et al.*, 1984). An undetermined species of the genus *Theraptus* (Hemiptera: Coreidae) in Kenya, that severely damages developing coconut fruits is controlled through predation by the ant *Oecophylla longinoda* Latrielle (Hymenoptera: Formicidae) (Way, 1951; 1953). *Oecophylla smaragdina* Fabricius (Hymenoptera: Formicidae) and other beneficial ant species protect coconut palms in the Solomon Islands from damage by the coreid *Amblypelta cocophaga* China (Hemiptera: Coreidae). Immature nutfall of coconuts caused by *A. cocophaga* depends indirectly on certain species of ants, some of which protect the palms from damage through predation on *A. cocophaga* while other species do not (Phillips, 1956; Brown, 1959; Greenslade, 1971). The native gray ant, *Formica aerata* Francoeur (Hymenoptera: Formicidae) is the most effective predator of the peach twig borer in Californian peach orchards (Daane & Dlott, 1998). In maize and grain sorghum crops, the ant *Dorylus helvolus* L. (Hymenoptera: Formicidae) was the most important predator of planted and naturally pupating bollworm, *Helicoverpa armigera* Hübner (Lepidoptera: Noctuidae), pupae (Watmough & Kfir, 1995). *Solenopsis geminata* and *Pheidole* spp. are important predators of rootworm eggs in Costa Rica (Risch, 1981). The impact of predatory ants on pest populations can be substantial, through good management strategies and the manipulation of their populations to the disadvantage of the pest species (Gotwald, 1986).

Although the beneficial effects of predatory ants in the control of soil-pupating citrus pests such as the Mediterranean fruit fly, false codling moth, *Cryptophlebia leucotreta* Meyrick (Lepidoptera: Tortricidae), and bollworm have been noted (Steyn, 1954a, b; Samways, 1982), the extent to which they control these pest species has not previously been quantified. These ants, more than likely, also have an important influence in the control of other economically important soil-pupating citrus pests such as citrus thrips, *Scirtothrips aurantii* Faure (Thysanoptera: Thripidae) and the Natal fruit fly, *Ceratitis rosa* Karsch (Diptera: Tephritidae).

1.2 Aims and Scope

If ants can be shown to be important predators of soil-pupating citrus pests,

- the use of ant bands as opposed to poisons will be strongly justified, so that beneficial species are left on the ground to prey on pest pupae
- careful management with regard to chemical control programs should be employed to maximise benefits from this opportunity
- a greater permanence of pest suppression should be obtained, resulting in increased crop yield
- pest management programs in other tree crops where these ants are present, should consider these benefits

1.2.1 The first aim of this study was to look at the ant community structure in orchards at Mosslands Farm in the Grahamstown area of the Eastern Cape. This was examined in relation to species composition, species diversity, orchard age and the effect of management practices on community structure.

1.2.2 The second aim was to quantify the beneficial effects of predatory ants in citrus orchards in order to refine their management and integrate it with other aspects of citrus crop management. This was done through:

- quantification of the predation of ants on bait pupae of pests like bollworm, false codling moth and fruit fly, both when they have access to the trees and when they are excluded from them;
- examination of how pest predation changes from month to month; and
- examination of pest predation in relation to the ant community structure.

Three non-continuous subunits in each of eight experimental citrus orchards of different ages were each assigned to a different treatment. In one subunit, the trees were banded, so that ants were prevented from foraging in the trees. In the second subunit, populations of *P. megacephala* and *A. custodiens* were poisoned so that their populations were significantly suppressed. The third subunit in each plot served as the untreated control. Ants were sampled by pitfall trapping in all the subunits. Bait pupae were planted in all the subunits, to check for the effect of predation in the relative absence of these two ant species and where they were prevented from foraging in the trees. Trapping times were synchronised with six of the eight predation trials. Three trials were conducted with bollworm and FCM pupae and two trials were conducted with fruit fly. The bollworm trials were conducted from December 2000 to February 2001, the FCM trials from March 2001 to May 2001 and the fruit fly trials from October 2001 to November 2001.

1.3 Predacious ant species - potential beneficials

1.3.1 The pugnacious ant, *Anoplolepis custodiens* (Smith)

Anoplolepis custodiens is distributed throughout the citrus production areas in South Africa (Samways *et al.*, 1982) with the exception of the Western Cape (Samways *et al.*, 1998). It is particularly abundant and widespread in the Eastern Cape (Steyn, 1954a; Myers, 1957) and in the summer-rainfall, savanna region (Samways *et al.*, 1998). The pugnacious ant reaches pest status principally from attending honeydew-producing Homoptera. It is a major pest in orchards throughout the country, causing infestations of citrus mealybug, *Planococcus citri* Risso (Hemiptera: Pseudococcidae) and *C. hesperidum*. A more serious problem, however, is that it causes coincident infestations of *A. aurantii* when foraging for honeydew and attending honeydew-producing species (Steyn, 1954a).

Anoplolepis custodiens is a highly predacious diurnal forager and the larvae are fed regurgitated honeydew (Steyn, 1954a). They have large subterranean nests, excavated in hard, loamy soils, with several entrances which are clean holes 3 to 4 mm in diameter (Steyn, 1954a; Samways *et al.*, 1998). Populations can fluctuate substantially depending principally on the availability of food, particularly honeydew. Their numbers decline dramatically in the absence of honeydew and other ant species then colonise the orchard, with the result that *A. custodiens* is kept at a low level, distributed in patches. Their major natural enemy is the competitive brown house ant, *P. megacephala*. These two species rarely interact but the result of this is an orchard completely dominated by one or the other (Samways *et al.*, 1998).

1.3.2 The brown house ant, *Pheidole megacephala* (Fabricius)

Pheidole megacephala is found in all the citrus-producing areas in South Africa (Samways *et al.*, 1982), with the exception of the Western Cape, but is only a major economic pest in certain geographical areas, particularly the Eastern Cape and KwaZulu-Natal (Samways *et al.*, 1998). Infestations of *P. megacephala* can be severe, arising from and resulting in outbreaks of honeydew-producing Homoptera. These ants attend *C. hesperidum*, soft green scale, *Pulvinaria aethiopica* De Lotto (Hemiptera: Coccidae) and mealybugs (Hemiptera: Pseudococidae) and are especially problematic, as with *A. custodiens*, in causing outbreaks of *A. aurantii* through disturbance of its major natural enemies (Steyn, 1954b; Samways *et al.*, 1998).

Pheidole megacephala is a predacious, largely nocturnal forager, collecting honeydew to feed to their larvae. They have large subterranean nests, often found around the bases of tree trunks. Fine particles of soil are excavated and dumped on the soil surface around a small entrance hole. The result is a small, distinctly circular crater about 30-40 mm (Samways *et al.*, 1998). Populations of *P. megacephala* decline in periods of drought, in winter in the summer-rainfall regions, and when there is a decline in honeydew resources. Their major natural enemies are other ants, but when present, *P. megacephala* is usually the dominant species (Samways *et al.*, 1998).

1.4 Pest species

1.4.1 False codling moth, *Cryptophlebia leucotreta* Meyrick

Cryptophlebia leucotreta is a major pest of cultivated crops in southern Africa, attacking many types of deciduous, tropical and subtropical fruits. It is particularly severe on citrus and is an important pest of citrus in all of the major citrus producing areas in South Africa (Quayle, 1941; Newton, 1998). Navel oranges appear to be the most heavily attacked and are susceptible from as early as November (Newton, 1998), when no more than 15-20 mm in diameter (Stofberg, 1954), and from then on throughout the season. Females produce up to 300 eggs, which are laid predominantly on the fruit surface. Eggs are usually laid singly (Annecke & Moran, 1982; Newton, 1998) but up to 65 eggs have been found on a single fruit (Stofberg, 1954). Cannibalism among young larvae ensures that usually only one larva matures in each fruit (Annecke & Moran, 1982).

Fruit damage is caused by penetration of the emerging larvae into the fruit, which leads to premature ripening, and fruit decay and abscission. The larvae burrow towards the fruit core or feed just below the fruit surface for 4 to 5 weeks, after which the mature larvae leave the fruit and pupate in loose soil, beneath surface debris or in cracks in the soil. The duration of the pupal stage is 29 to 40 days in winter and 21 to 24 days in summer (Newton, 1998). The pupae are 6 to 7 mm in length (Gunn, 1921).

Orchard sanitation, whereby infested fruits are removed and destroyed before the larvae emerge to pupate in the soil, has remained the most important recommended method for suppressing this pest throughout the country (Annecke & Moran, 1982; Newton, 1998). Natural enemies of *C. leucotreta* such as egg and larval parasitoids do not provide adequate control and results of the release of the biological control agent, *Trichogrammatoidea cryptophlebia* Nagaraja (Hymenoptera: Trichogrammatidae) have been unpredictable and often unsatisfactory. An IPM approach is recommended for control of this pest in citrus (Newton, 1998).

1.4.2 The Mediterranean Fruit Fly, *Ceratitis capitata* (Wiedemann)

Ceratitis capitata is the most serious pest in the family Tephritidae and is widespread throughout South Africa. This species is highly polyphagous, accepting many types of subtropical, tropical and deciduous fruits as food (Annecke & Moran, 1982; Du Toit, 1998). Med flies, as they are commonly known, are active throughout the year. Early citrus cultivars such as navels are particularly susceptible to fruit fly attacks. In citrus, damage is mainly caused indirectly through fungal infection. Eggs are laid in clumps in the rind tissue but these seldom develop to the adult stage in citrus fruits. However, frequent punctures made by the ovipositor of the female are invaded by fungal spores of the green mould, *Penicillium digitatum,* which causes the fruit to rot before the crop is picked (Annecke & Moran, 1982).

In citrus, the larvae usually die as a result of the oil in the rind of fruit (Annecke & Moran, 1982). However, if they survive, the larvae develop inside the fruit, completing their development in 10 to 20 days. The mature larvae leave the fruit and pupation takes place in the soil, the duration of which is 10 to 15 days. The puparium is 10 to 15 mm in length (Du Toit, 1998).

Three parasitoids native to South Africa attack either the larval or pupal stages of *C. capitata,* but they are unable to control this pest effectively on citrus (Annecke & Moran, 1982; Du Toit, 1998). A combination of orchard sanitation, the destruction of useless host plants, regular bait sprays and the monitoring of population build-ups with pheromone traps is needed for effective control of this pest (Du Toit, 1998).

1.4.3 Bollworm, *Helicoverpa armigera* Hübner

Helicoverpa armigera occurs throughout South Africa and is considered to be one of the most problematic pests of citrus (Annecke & Moran, 1982; Vermeulen & Bedford, 1998). In addition to citrus, *H. armigera* attacks a variety of other crops such as tobacco, wheat, maize, tomatoes, beans, peas, lupins and sorghum (Vermeulen & Bedford, 1998). The moths are attracted to citrus in spring during the blossoming period. Eggs are laid singly on closed buds and on young leaves. The larvae feed on open blossoms and fruit, moving from one to another, without destroying them completely (Vermeulen & Bedford, 1998). Fruit is rendered unmarketable though the characteristic rind damage caused by feeding (Annecke & Moran, 1982).

The larvae pass through six instars in approximately 29 days and then crawl or drop to the ground to pupate in the soil (Reed, 1965; Vermeulen & Bedford, 1998). The duration of the pupal stage is 15.5 days and the pupae are 13.5 to 18 mm in length (Vermeulen & Bedford, 1998).

For control of this pest, the application of insecticides is necessary in individual orchards when populations reach levels that can cause economic injury. The indigenous natural enemies of *H.armigera* are unable to control the periodic outbreaks that occur in citrus (Vermeulen & Bedford, 1998).

1.5 Study site

This study was conducted on Mosslands Farm, which lies approximately 20 km west of Grahamstown in the Eastern Cape, South Africa (33º24′S 26º26′E). Two experimental plots for each of four different ages of trees were selected. The ages of the trees at the start of the study in 2000 were 2, 4, 15 and 30 years old. All eight plots were planted with navel trees and were selected from those available throughout the farm. The numbers of trees and the number of rows in each plot and the years in which they were planted are tabulated in Table 1.1. The position of the plots are indicated on a map of Mosslands Farm (Fig. 1.1).

All eight plots were treated with the herbicide Roundup (glyphosate) three to four times annually. Plots 2a, 2b, 4a and 4b received no chemical treatment since planting. Plots 30a and 30b were sprayed with Acarol (bromopropylate which is a dibrome hydrocarbon derivative) in 1994 and with Ultracide in 1996. Plots 30a, 30b, 15a and 15b received an application of Acarol in 1998, of Tartox (tartar emetic bait which is an antimony compound) in 1999, of Tokuthion (prothiophos which is an organophosphate insecticide) in October 2000 and of Tartox again in December 2000. All four of these plots were treated with a mineral oil spray in August 2000.

Acarol appears to be very safe for IPM (Bedford *et al.*, 1992; Bedford, 1998c). Tartox is so specific that it controls only citrus thrips (Bedford *et al.*, 1992; Bedford, 1998c), however, because it is applied with sugar, parasitoids are attracted to feed on it, which can cause reductions in parasitoid numbers. However, if it is not applied more than three times in a season, it is considered to be compatible with IPM (Sean Moore, pers. comm.). Tokuthion is toxic to predatory mites of citrus thrips and phytophagous mites (Grout *et al.*, 1996) and is therefore not IPM compatible. With the exception of the Tokuthion application, all of the chemicals applied to plots 30a, 30b, 15a and 15b are compatible with an IPM approach. Large numbers of honeydew producers were never apparent in any of the experimental orchards and *P. megacephala* and *A. custodiens* were not considered to be major pests in these orchards.

All of the plots were similar in having grasses growing between the rows of trees. Bait traps and pitfall traps were placed in close proximity to the trunks of the trees. The habitat in plots 30a, 30b, 15a and 15b had 100% shade provided by the tree canopy, was covered with leaf litter and the soil was soft and moist. The habitat in plots 4a, 4b, 2a and 2b had little or no shade on a bare, dry sandy soil surface.

Table 1.1 Number of rows and the number of trees in each of the experimental orchards and the years in which they were planted

Plot	Year planted	Rows x trees	No. of trees
30a	1970	12 x 15	180
30b	1970	12 x 15	180
15a	1985	10 x 12	120
15b	1985	12 x 13	156
4a	1996	7 x 13	91
4b	1996	19 x 47	893
2a	1998	9 x 23	207
2b	1998	16 x 21	336

Fig. 1.1 Map of Mosslands Farm, indicating the position of the experimental orchards

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The effect of orchard age and ant management practices on the community structure of ants in citrus orchards

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Summary

Epigaeic ant communities were sampled by pitfall trapping in two treated subunits and a control subunit in 2-, 4-, 15- and 30-year-old citrus orchards. In one of the treated subunits in each orchard, the trees were banded so that the ants were excluded from the trees and in the second treated subunit in each plot, two ant species, *Pheidole megacephala* (Fabricius) and *Anoplolepis custodiens* (Smith) were poisoned so that their populations were significantly suppressed. Trapping was done for a period of five days, once monthly from December 2000 to April 2001 and then again in November 2001. *Pheidole megacephala* was the exclusive dominant ant in all of the orchards. Community composition did not change dramatically with an increase in the age of the orchards but species diversity and species abundance did. Rank-abundance plots showed that community diversity was lowest in the 30-year-old plots and highest in the 2-year-old plots. Diversity indices and equitability measures indicated that diversity and equitability were highest in the poisoned subunits and lowest in the banded subunits. Principle component analysis showed that the poisoned subunits were similar and distinct in species composition, that there was significant monthly variation, and that community stability increases with an increase in orchard age. Ant communities in citrus orchards are organized by ecological processes such as succession and external influences such as ant management practices.

2.1 Introduction

Ants are a major component of the citrus orchard fauna (Samways *et al.*, 1982) and are abundant both as individuals and as species (Samways, 1983b; 1990a). The organisation of ant communities is influenced by a number of factors. Inter- and intra-specific interactions such as competition for space and resources influence their distribution patterns, while dominant species affect the community composition and abundances of other ant species in the community (Hölldobler & Wilson, 1990). Habitat (Samways, 1983b) and microhabitat (Jeanne, 1979) type influence community diversity. In citrus orchards, external influences such as pest management affect ant assemblage patterns on the orchard floor (Samways, 1981).

Ants in citrus orchards forage in the trees and on the ground (Samways *et al.*, 1982). Most of the tree-foraging species are harmless to citrus, but two species, *Pheidole megacephala* (Fabricius) and *Anoplolepis custodiens* (Smith), reach economic pest status through precipitating outbreaks of homopterous pests. Ants are well-known mutualists of honeydew-producing homopterans (Way, 1963), collecting the honeydew excreted by aphids, soft scales and mealybugs to feed to their larvae (Steyn, 1954a; Samways *et al.*, 1998). The ants interfere with the activities of natural enemies of these pests and those of more serious pests such as red scale, *Aonidiella aurantii* Maskell (Steyn, 1954a, b; Bedford, 1968). Thus ant control in citrus orchards is essential. Chemical applications and trunk barriers (ant bands) are used for the control of these two species in citrus (Samways *et al.*, 1998).

In this study, the epigaeic ant community structure in orchards of differing ages was examined in relation to species composition and species diversity. The effect of control methods for *P. megacephala* and *A. custodiens* on the ant communities was examined.

2.2 Materials and Methods

Ant communities were sampled at Mosslands Farm (33°24′S 26°26′E), which lies approximately 20 km west of Grahamstown in the Eastern Cape, South Africa. Two plots (orchards) of navel (C*itrus sinensis*) trees of each of the ages 2, 4, 15 and 30 years old were selected from those available on the farm (Fig. 1.1; Table 1.1).

Three non-overlapping and non-adjacent subunits, each consisting of a block of 16 trees (Fig. 2.1), were chosen in each of these plots as individual sampling sites and were assigned to different treatments. In one subunit, ants were excluded from the trees with the use of ant bands. These bands were placed halfway up the trunk of the tree and consist of a layer of bidim or polyester fibre which is held in place by two to three layers of stretch wrap plastic. A third layer - Plantex (polybutene and wax compound), which serves as a sticky barrier lasting for several months, is applied on top of the plastic and is effective in preventing ants from entering the trees. This band 'Ant Bar 1.2.3.' (supplied by KatCo) was recommended by Samways and Buitendag (1986) and is a highly effective method of keeping ants out of trees (Samways, 1990a). Ant bands were checked regularly and the sticky barrier reapplied if necessary. Anything that may have provided the ants with an alternative route up the tree, such as tree skirtings and weed bridges, were removed (Samways, 1990a). In a second subunit, populations of *P. megacephala* and *A. custodiens* were poisoned so that their populations were significantly suppressed. Amdro (Hydramethylnon ant-bait) was applied at 0.2 g per square metre to eliminate *P. megacephala* and parathion, applied at a rate of 7 ml per litre of water, was sprayed into the nest entrances of *A. custodiens*. Amdro, which is a proprietary bait that was developed for the control of the fire ant *Solenopsis geminata* Buren, is effective in suppressing *P. megacephala* (Samways, 1985; Petty, 1993). The application rate of Amdro was followed from Petty (1993; pers. comm.) and was effective at this dosage, and the application rate of parathion was followed on the advice of the farm owner, Rob Moss (pers. comm.). Although the application rate of the parathion is lower than the recommended concentration, the farm owner found it to be effective at this dosage. These treatments were reapplied whenever ant reinvasion was observed. A third subunit in each plot served as an untreated control.

Ants were sampled by pitfall trapping. This method is used to estimate the abundance and species composition of ground-surface active ants in an area (Bestelmeyer *et al.*, 2000). Majer (1997) found that using only pitfall traps tends to undersample the ant community and that this method has several disadvantages such as differing sensitivities of the various species to traps (Southwood, 1978). However, Samways (1983b) found that in citrus orchards in Nelspruit, South Africa, pitfall traps caught more individuals and more species of ants with greater consistency when compared with other methods. Also, this method has been widely used for sampling epigaeic ant faunas (Donnelly & Giliomee, 1985a, b; Samways, 1981, 1983b, 1990b; Bestelmeyer & Schooley, 1999). Modified from Samways (1981), each trap consisted of a glass test-tube (23 x 150 mm) sunk vertically within a plastic irrigation pipe sheath so that the lip of the test-tube was flush with the soil surface. Each test-tube contained a 2 cm depth of ethylene-glycol as the killing-preserving agent. A set of eight pitfall traps was arranged at each individual sampling site (each subunit), making 24 traps in each plot and 192 traps in total. At each set, four traps were placed on the inner side of the outer and the inner four trees, in close proximity to the trunks of the trees (Fig. 2.1). Traps were in use for a period of 5 days at a time at monthly intervals. Three to four days is sufficient for optimal trapping (Jansen & Metz, 1979). Samples were collected once monthly from December 2000 to April 2001, and in November 2001. No samples were taken from May 2001 to October 2001 as ant activity levels decline in the winter months (Samways, 1990b). After trapping, the test-tubes were taken back to the laboratory and the ants collected and preserved in 5 ml Eppendorf tubes in 70% alcohol. The ants were identified to genus and, where possible, to species using Arnold's (1915) monograph of the South African Formicidae. Voucher specimens were sent to the South African Museum for confirmation of the identifications, and are now held there as part of the reference collection.

The ant communities were described in terms of species diversity and species composition. Rank-abundance plots were used to illustrate graphically the diversity of the ant fauna sampled in each plot, and the diversity of the community on the farm as a whole. The abundance of each species was plotted on a logarithmic ($\log_{10}$) scale against the species rank sequence. These plots show visually the two aspects of community diversity (May, 1981). The first aspect of community diversity is species richness, which is the total number of species present (S). The second aspect is equitability (evenness), which expresses how evenly the individuals are distributed among the different species (Clark & Warwick, 1994).

The reciprocal of Simpson's diversity index (1/D), the Shannon-Wiener diversity index (H′) and their evenness values (Krebs, 1989; Begon *et al.*, 1990) were used to show the diversity and equitability of the communities in the banded, control and poisoned subunits. The indices and evenness measures were calculated in Krebs' software package

- Ecological Methodology, version 0.94 - and are tabulated in Appendix 1. The reciprocal of Simpson's diversity index was used so that a higher number means higher diversity (Longino, 2000). A multi-way ANOVA (Zar, 1974) was used to test for statistically significant differences between these measures in the different aged plots and in the treated subunits. Ant communities sampled in the different months and in the treated subunits were analysed using principle component analysis and Pearson's correlation analysis. A three-way ANOVA (Zar, 1974) was used to test for statistically significant differences between the component scores of the first principle component for age, treatment and month. A one-way ANOVA (Zar, 1974) was used to test for statistically significant differences between the component scores of the second principle component and orchard age. All statistics tests were done in Statistica, version 5.5.

2.3 Results

A total of 21 550 individuals in 16 species were collected (Table 2.1). The Myrmicinae and Formicinae were the dominant subfamilies. *Pheidole megacephala* was the exclusive dominant ant. *Monomorium opacior* Forel and *Lepisiota incisa* Forel were relatively abundant. *Tetramorium mossamedense* Forel, *Anoplolepis custodiens* (Smith), *Camponotus* sp. (near *maculatus* Fabricius), *Technomyrmex* sp., and *Dorylus helvolus* Linnaeus were conspicuous as moderately abundant species. *Monomorium* sp. (near *taedium* Bolton), *Camponotus irredux* Forel, *Leptogenys attenuata* F. Smith and *Leptogenys castanea* Mayr were relatively scarce and *Messor capensis* Mayr, *Crematogaster liengmei* Forel, *Plectroctena mandibularis* F. Smith and *Aenictus rotundatus* Mayr were extremely rare. Table 2.2 shows the species and the numbers of individuals sampled in all of the plots. There was extreme dominance in plots 30a, 30b, 4a, 4b, 2a and 2b by *P. megacephala.* Although this species was also dominant in plots 15a and 15b, their populations were substantially smaller than in the other plots. There was far greater equitability in plots 15a, 15b, 4b, 2a and 2b than in plots 30a, 30b, and 4a. *Lepisiota incisa* was the second or third most abundant species in all of the plots with the exception of plot 15b. *Monomorium opacior* was the second most abundant species in the 15-year-old plots and the 2-year-old plots. All of the paired plots of the different ages were similar in having at least four of the six most abundant species in common. *Pheidole* *megacephala*, *L. incisa*, *M. opacior*, and *T. mossamedense* were among the most abundant species in all of the plots.

Table 2.3 shows the ant species composition and abundance in the treated subunits of all of the plots. Species richness was highest in the control subunits (mean S = 16), and was lower and similar in the banded and poisoned subunits (mean S = 13). *Monomorium opacior* was the second most abundant species in the banded and control subunits and was relatively scarce in the poisoned subunits. Two of the rare species, *C. liengmei* and *M. capensis*, were found only in the control subunits. The abundance of *A. custodiens* in the poisoned subunits was not considerably lower than in the control subunits. Eighty-three specimens of this species were collected in the poisoned subunit of plot 4b in December 2000, which represents more than half of the total number collected in all the poisoned subunits throughout the sampling period. The poison application had obviously not yet taken effect and high numbers of *A. custodiens* were collected at one sampling point. Overall ant abundance in the poisoned subunits was low in comparison to the banded and control subunits. The poisoned subunits were the most equitable and the most diverse of the three treated subunits. Equitability was higher in the control subunits than in the banded subunits, thus diversity was lowest in the banded subunits. There was extreme dominance by *P. megacephala* in the banded and control subunits. In the poisoned subunits, where populations of *P. megacephala* were significantly suppressed, individuals of species were more evenly spread within the community.

A rank-abundance curve (Fig. 2.2) shows the richness and equitability of the sampling sites together. One species (*P. megacephala*) was the exclusive dominant ant. Equitability was good, and thus the overall community was quite diverse. Rank-abundance curves were fitted to the ant community within each plot (Fig. 2.3). These plots are useful as a preliminary exploration of community structure (Samways, 1983b). Plots 30a, 30b, and 4a have the lowest species richness, the lowest equitability and therefore the lowest diversity of all of the plots, with extreme dominance by *P. megacephala*. Equitability and species richness were higher in plots 15a, 15b and 4b. Plots 2a and 2b have the highest species richness, the highest equitability and therefore the most diverse communities.

Simpson's and the Shannon-Wiener diversity indices and their evenness values confirm the qualitative observations made with the rank-abundance plots. Simpson's diversity indices for the banded, control and poisoned subunits of the different aged plots are plotted in Fig. 2.4.

There are significant differences in community diversity in the treated subunits (F = 8.144; p < 0.001) and in the different aged plots (F = 5.581; p = 0.012). Community diversity in the poisoned subunits was higher than in the banded and control subunits in all of the plots (Fig. 2.4). Diversity was lowest in the 30-year-old plots in all of the subunits. Diversity in the banded and control subunits was highest in the control subunits of the plots with 2- and 15-year-old trees. There is a general trend for community diversity to decrease with an increase in the age of the trees (Fig. 2.4). Diversity in the banded, control and poisoned subunits of the plots with 4-year-old trees and the banded and control subunits of the plots with 15-year-old trees was similar. Equitability of the communities was significantly different between the treated subunits (F = 16.554; p < 0.001) and the different aged plots (F = 21.317; p < 0.001). The poisoned subunits had the highest equitability of the treated subunits, while the banded subunits had the lowest (Fig. 2.5). Communities in the 30-year-old plots were the least equitable and therefore, the least diverse. There is the same general trend for equitability to decrease with an increase in the age of the trees.

The Shannon-Wiener diversity indices for the banded, control and poisoned subunits in the different aged plots are plotted in Fig. 2.6. Significant differences in community diversity were found between the treated subunits (F = 12.263; p < 0.001) and the different aged plots (F = 20.583; p < 0.001). The general trend is the same, but there are a few differences. Community diversity in the poisoned subunits in plots 15a and 15b is much lower than the Simpson's diversity index given for those subunits. Diversity of the control subunits of the 2-year-old plots is higher than was given for Simpson's index. The Shannon-Wiener diversity index for the poisoned subunits of the 30-year-old plots is much higher than Simpson's index. Fig. 2.7 shows the evenness measures from the Shannon-Wiener diversity indices. Significant differences in the equitability of the communities were found between the treated subunits (F = 12.272; p < 0.001) and the different aged plots (F = 20.536; p < 0.001). The pattern is exactly the same as that of

Simpson's evenness values, but the Shannon-Wiener evenness values are much lower than Simpson's evenness values.

Principle component analysis was carried out on the ant communities. The first axis summarized 12.95 % of the variation and the second axis 11.02 % (Fig. 2.8; Fig. 2.9; Fig. 2.10). *Monomorium opacior*, *L. incisa*, *Monomorium* sp. and *T. mossamedense*, were highly correlated with the component weights of the first axis (Table 2.4). *Camponotus* sp., *D. helvolus*, *M. capensis* and *P. megacephala* were weakly correlated with the first component. *Technomyrmex* sp., *A. custodiens*, *D. helvolus*, *L. attenuata*, *L. castanea*, *L. incisa* and *P. megacephala* were highly correlated with the component weights of the second axis (Table 2.4). *Camponotus irredux*, *Camponotus* sp., *M. capensis*, *M. opacior* and *P. mandibularis* were weakly correlated with the second component.

Camponotus sp., *D. helvolus*, *L. incisa*, *M. capensis*, *M. opacior*, *Monomorium* sp., *P. megacephala* and *T. mossamedense* characterized the positive side of the first axis. *A. custodiens*, *L. incisa*, *P. megacephala*, *P. mandibularis* and *Technomyrmex* sp. characterized the positive side of the second axis while *Camponotus irredux*, *Camponotus* sp., *D. helvolus*, *L. attenuata*, *L. castanea*, *M. capensis* and *M. opacior* characterized the negative side (Table 2.4).

There is more distinct separation of the samples from the different-aged plots along the first axis than the second axis (Fig. 2.8). The 30-year-old plots formed a discreet group and the 15-year-old plots were relatively well grouped along the first axis. There was more variation in community assemblage in the 2- and 4-year-old plots than in the 15- and 30-year-old plots. The component scores of the first principle component were significantly lower ($F = 11.458$; $p < 0.001$) in the 15- and 30-year-old plots than in the 2- and 4-year old plots (Fig. 2.12). The component scores of the second principle component were significantly higher ($F = 12.889$; $p < 0.001$) in the 4- and 30-year-old plots than in the 2- and 15-year-old plots (Fig. 2.13).

Separation of the samples from the different months is better along the first axis than the second axis, but there is no significant overall pattern. The November samples of the ant community are relatively well grouped and were thus similar and distinct in species composition. The samples from each month were poorly differentiated along the second axis (Fig. 2.9). There were significant differences (Fig. 2.11: F = 2.452; p = 0.037; Fig. 2.12: F = 3.020; p = 0.013) between the component scores of the first principle component for the different months. March was the most variable in species composition and March and November were significantly different from the rest of the months.

Plots of the first two principle components classified according to the treated subunits showed good separation of the treatments on the first axis (Fig. 2.10). The poisoned subunits formed a discreet group and the banded and control subunits were relatively well grouped along the first axis. *Technomyrmex* sp. was characteristic of the poisoned subunits while *L. incisa*, *T. mossamedense*, *P. megacephala*, *M. opacior*, *Monomorium* sp., *D. helvolus* and *Camponotus* sp. were associated with the banded and control subunits (Fig. 2.10). The component scores of the first principle component were significantly lower (F = 23.347; p <, 0.001) in the poisoned subunits, than in the banded and control subunits (Fig. 2.11).

2.4 Discussion

The ant community of the study area, as represented in the eight orchards that were sampled, was quite diverse. *Pheidole megacephala* predominated numerically and was thus exclusively the dominant ant species. Only two main habitat types were sampled: young and mature orchards. The habitat in the mature orchards (plots 30a, 30b, 15a and 15b) was completely shaded by the tree canopy, was covered with leaf litter and the soil was soft and moist. The habitat in the young citrus orchards (4a, 4b, 2a and 2b) had little or no shade on a bare, dry, sandy soil surface. Microhabitat specificity (Jeanne, 1979) and habitat preference (Samways, 1983b) among ants is marked. Species richness may have been higher if more habitat types within the orchards, such as between the trees as opposed to under them, or the grasses growing between the rows of trees, were sampled. Samways (1983b) found species richness to be considerably higher in grassland habitats associated with citrus, than species richness within the orchards, under the tree canopy.

Effect of orchard age on species composition and diversity patterns

Species composition does not seem to change dramatically with increasing age of citrus, although there is variation in the relative abundances of the different species. Brian *et al.*

(1976) found that species composition in a heathland, two years and ten years after a burn, was similar, but the abundance of the species differed between the habitats. Donnelly & Giliomee (1985a) found that species composition of ants in 37-year-old fynbos and young firebreak sites was not vastly different, but the frequency of occurrence of the various species changed. These findings have been attributed to a changing habitat (associated with a change in the plants), which fluctuates between a state favouring some species and a state favouring others. The change in habitat (such as the soil conditions and the amount of shade provided by the trees) associated with an increase in age of citrus influences the abundance of species on the orchard floor.

The rank-abundance plots show similar patterns of diversity in the plots of the same age, particularly in the youngest (2a and 2b) and oldest (30a and 30b) plots. This emphasizes the influence of habitat type on community diversity. Insect diversity has been correlated with plant species diversity and plant structural diversity (Murdoch *et al.*, 1972) and Samways (1990b) has noted the change in ant assemblage with plant community succession.

Diversity was highest in the youngest plots, which can be considered to be disturbed habitats, and diversity was lowest in the oldest plots that are more stable habitats and can be considered to be the climax community. Diversity in the 4-year-old plots and 15-year-old plots was variable and intermediate between the 2-year-old and 30-year-old plots. Perhaps a likely scenario is that, after a disturbance (in this case being the replanting of an orchard), there is recolonization by all species to which that habitat is favourable. As the orchard matures, the changing conditions (with the changing habitat) become less favourable to some species, and their numbers decline or they disappear from the habitat altogether. Risch & Carroll (1982a) found that immediately after replanting a ‘forest milpa’, made by cutting and burning a 40-year-old forest, and a ‘field milpa’ made by ploughing 1-year-old second growth, with maize, squash and beans, the same number of species occurred in each milpa type, and thereafter the ant faunas in the two habitats diverged. Donnelly & Giliomee (1985b) found that diversity of the epigaeic ant fauna in fynbos was higher after burning the vegetation than it was before. Inter-specific interactions then also play a role in structuring the community. During the successional process, the species that are stronger competitors start to replace the early colonizers as population densities increase and the habitat changes. There is much more variation in community structure in the younger orchards and it seems that as the orchards mature, stability increases until they reach a climax community. The lower diversity in the mature orchards may also partly be attributed to the sampling method used in the two habitat types. The leaf litter on the ground in the mature orchards would have created a 3-dimensional trapping pattern as opposed to the 2-dimensional trapping pattern in the young orchards with bare ground. However, at the start of trapping, leaf litter from around the traps was cleared away, so this would not have had a significant impact on the numbers and types of species collected.

Effect of the time of year on community structure

There was significant monthly variation in species composition. However, the November samples were the most distinct in species composition and these samples were taken out of the monthly sequence after the autumn/winter period. Different species may have different sensitivities to temporal variation. The November samples may have consisted of species that maintained their population levels through the winter period.

Effect of ant management strategies on community structure

Clearly, methods of ant control also have an influence on ant diversity patterns on the orchard floor. Community composition in the poisoned subunits was significantly different to community composition in the banded and control subunits. The higher diversity and equitability in the poisoned subunits could partly be attributed to the suppression of *P. megacephala* populations. Dominant species form the core of the local ant community, affecting the composition and abundance of other ant species (Hölldobler & Wilson, 1990). Greenslade (1971) found that in coconut plantations in the Solomon Islands, ant community diversity increased when populations of a dominant species, *Anoplolepis longipes* Jerdon declined, and diversity decreased when its populations flourished.

The dominance of *P. megacephala* in the banded and control subunits and its reduced dominance in the poisoned subunits would have influenced the diversity indices. Simpson's index is strongly influenced by the relative abundance of the few most abundant species and the Shannon-Wiener index is influenced by both richness and dominant species (Longino, 2000).

It is evident too that the poison applications had an effect on community composition and species abundance. It is unlikely that the parathion would have had a significant direct effect on the rest of the ant community as it was sprayed directly into nest entrances, but the Amdro was possibly attractive to a variety of other species, as well as *P. megacephala*. The abundance of some species in the poisoned subunits varied considerably when compared to their abundance in the banded and control subunits, possibly either due to the decline in populations of *P. megacephala* or due to the effect of the Amdro. *Monomorium opacior*, *T. mossamedense*, *Monomorium* sp. and *L.incisa* were considerably less abundant in the poisoned subunits and were characteristic of the banded and control subunits. It is likely that these species were either eating the Amdro or that at they co-exist favourably with *P. megacephala* and were thus scarce where population levels of this species were low, or both.

With the suppression of populations of *P. megacephala*, the availability of space and resources to other species would have increased. Considerably higher numbers of *Technomyrmex* sp. were found in the poisoned subunits and this species was characteristic of the poisoned subunits. Seemingly, it was not affected by the Amdro and was able to capitalize on the newfound space and resources. The abundance of other species was relatively constant in the different subunits and was thus not affected by the Amdro or the population levels of *P. megacephala*.

Samways *et al.* (1982) found that 23 of the 123 species found in citrus orchards throughout South Africa forage in the trees (although not all attend Homoptera). *Pheidole megacephala*, *A. custodiens* and *C.* cf. *maculatus* forage in citrus trees. The abundance of *Camponotus* sp. and particularly of *A. custodiens* was considerably lower in the banded subunits than in the control subunits. It seems that banding of the trees has an influence on the abundance of tree-foraging species and clearly has an influence on diversity and equitability. Banding of the trees removes a microhabitat from the environment, reducing niche and resource availability that would lead to lower diversity. The activity levels of these two species in the banded subunits may have been lowered in response to the removal of a food source from the environment, which may also account for their lower abundance in the banded subunits than in the control subunits. *Technomyrmex* sp. was significantly less abundant in the banded subunits than in the control and poisoned subunits. It seems that this species was also affected by the prevention of foraging in the trees. As the identification of this species is uncertain, it cannot be said whether it is definitely a tree-forager, but Samways *et al.* (1982) found *Technomyrmex albiceps* Smith to forage in citrus trees. It is interesting that the abundance of *P. megacephala* was slightly higher in the banded subunits than in the control subunits. This emphasizes the fact that this species is able to make use of other resources to sustain such high population levels.

Community structure

Pheidole megacephala had a significant influence on the diversity patterns seen in the different orchards. We have seen that ants are sensitive to habitat and microhabitat type. However, eurytopic species, such as *P. megacephala* are able to tolerate a wide range of variations in environmental conditions that, in spatial terms, allows them to be more abundant (Samways, 1990b). A pattern similar to that seen in these orchards, particularly in 30a and 30b, was evident in a guava orchard (Samways *et al.*, 1981) where there was extreme dominance by *A. custodiens*, and although three other species co-existed and were not outcompeted by *A. custodiens*, they were extremely rare. Ample mealybug resources supported the high population levels of *A. custodiens* (Samways *et al.*, 1981). High population levels of honeydew-producers were not apparent in the trees in the experimental orchards, thus some other resource on the orchard floor, honeydew or otherwise must have sustained these extremely high populations of *P. megacephala*. Orchard management practices may have had an influence on the dominance pattern. Samways (1981) found *P. megacephala* to be the dominant species in orchards under biological control (Samways, 1981) as was the case in these experimental plots.

Another possible contributing factor to the extreme dominance of *P. megacephala* could have been the absence of other potentially dominant species. Ants show high levels of inter-specific competition (Hölldobler & Lumsden, 1980) and in insects, competition can be strongly asymmetrical (Lawton & Hassell, 1981) leading to complete amensalism (Lawton & Hassell, 1981; Samways, 1983c). Amensalism is a one-sided competitive interaction in which one species has a negative effect on another but there is no detectable reciprocal effect (Morin, 1999; Lawton & Hassell, 1981). *Pheidole megacephala* is often dominant in citrus orchards (Samways, 1981; 1983b) but can be outcompeted by other potentially dominant species such as *Myrmicaria natalensis* Smith (Samways, 1983c) and *A. custodiens* (in areas where there are abundant honeydew resources) (Samways, 1983b). In the absence of abundant honeydew resources in the experimental orchards, *A. custodiens* seemed to remain at low population levels and was thus unable to be a strong competitor of *P. megacephala*. The absence of *M. natalensis* in the study area surely contributed to the exclusive dominance by *P. megacephala*.

There is substantial evidence that ants are distributed in a mosaic pattern, with different ants occupying different habitats within an area and there is a change in dominant species with a change in habitat (Greenslade, 1971; Majer, 1972; Leston, 1973; Room, 1975; Samways, 1983b). It cannot be said whether this spatial distribution pattern was evident in these orchards, as different habitat types within the orchards were not sampled. *Pheidole megacephala* can be extremely common but is only dominant in certain habitats. However, no mosaic pattern was evident in an orchard under biological control - *P. megacephala* dominated throughout (Samways, 1983b).

Communities are organised by a complex set of interactions that all have an influence in determining community structure. In terms of ecology, these results are significant as they show that ant management practices have a significant influence on ant species diversity. Ant banding leads to lower diversity and poisoning leads to higher diversity. Whatever the out come, the patterns are different to those seen in the control subunits where conditions were "normal". Poisoning not only affects diversity, it has an effect on non-target species in the community, and has a positive influence on soil-pupating pests (chapter 3). Thus, in ecological and economic terms, banding is preferable to poisoning as a method of ant control. The economic significance of these results is that *P. megacephala*, which is a potential pest in citrus orchards, can be extremely abundant. However, Samways (1981) found that control of this species in orchards under biological control is not necessary. He suggested that in orchards under stable biological control of *A. aurantii*, there are insignificant numbers of honeydew-producers to attract the ants in large numbers into the trees. Despite the fact that *P. megacephala* was so abundant in these orchards, it was not a pest and high numbers of honeydew-producers were never apparent in any of the experimental orchards. In Samways' (1981) biological control orchards, there was apparently a plentiful supply of food among the grasses and herbs on the orchard floor between the rows of trees, unlike the situation in other orchards with clean weeding. In addition to this, the economic significance of these results is that *P. megacephala* is an important predator of soil-pupating citrus pests (chapter 3) and thus its prominence in citrus orchards will be beneficial to the crop.

Table 2.1 Ant species and the total number of individuals sampled by pitfall trapping in all experimental plots, at Mosslands Farm (December 2000 – April 2001 and November 2001)

Species	***N***
MYRMICINAE	
Pheidole megacephala (Fabricius)	17949
Monomorium opacior Forel	1259
Tetramorium mossamedense Forel	297
Monomorium sp. (near *taedium* Bolton)	32
Messor capensis (Mayr)	1
Crematogaster liengmei Forel	2
FORMICINAE	
Lepisiota incisa (Forel)	714
Anoplolepis custodiens (Smith)	321
Camponotus sp. (near *maculatus* (Fabricius))	222
Camponotus irredux	37
PONERINAE	
Leptogenys attenuata (F. Smith)	19
Leptogenys castanea (Mayr)	11
Plectroctena mandibularis (F. Smith)	2
DOLICHODERINAE	
Technomyrmex sp.	464
DORYLINAE	
Dorylus helvolus (Linnaeus)	215
AENICTINAE	
Aenictus rotundatus (Mayr)	5
S = 16	*N* = 21550

Table 2.2 Abundance of ant species measured by pitfall trapping in orchards of different ages, at Mosslands Farm (December 2000 – April 2001 and November 2001)

Species	**30a**	**30b**	**15a**	**15b**	**4a**	**4b**	**2a**	**2b**
P. megacephala	3399	3823	852	474	5366	1411	1344	1280
M. opacior	13	30	225	181	105	130	411	164
T. mossamedense	1	6	21	25	28	80	74	62
Monomorium sp.	1	1	2	2	4	8	5	9
M capensis	0	0	1	0	0	0	0	0
C. liengmei	0	0	0	0	0	0	0	2
L. incisa	34	34	34	3	173	196	139	101
A. custodiens.	2	0	54	1	116	84	19	45
Camponotus sp.	17	6	12	23	54	25	28	57
C. irredux	0	6	0	10	4	0	12	5
L. attenuata	0	0	1	11	0	0	1	6
L. castanea	0	2	0	7	0	1	0	1
P. mandibularis	0	0	1	0	0	1	0	0
Technomyrmex sp.	3	5	1	0	28	352	36	39
D. helvolus	5	10	82	38	5	3	66	6
A. rotundatus	0	0	0	0	0	3	2	0
No. of species (S)	9	10	12	11	10	12	12	13
Total no. of individuals (*N*)	3475	3923	1286	775	5883	2294	2137	1777

Table 2.3 Ant species composition and abundance measured by pitfall trapping in the treated and untreated subunits of all of the experimental plots at Mosslands Farm (December 2000 – April 2001 and November 2001)

Species	**Banded**	**Control**	**Poisoned**
P. megacephala	9215	8160	574
M. opacior	611	593	55
T. mossamedense	126	161	10
Monomorium sp.	18	13	1
M capensis	0	1	0
C. liengmei	0	2	0
L. incise	253	348	113
A. custodiens.	4	175	142
Camponotus sp.	52	108	62
C. irredux	11	12	14
L. attenuate	3	4	12
L. castanea	2	6	3
P. mandibularis	0	1	1
Technomyrmex sp.	69	104	291
D. helvolus	82	92	41
A. rotundatus	3	2	0
No. of species (S)	13	16	13
Total no. of individuals (*N*)	10449	9782	1319

Table 2.4 Pearson's correlations of the first two principle components from a principle component analysis of the ant community with the abundance of the individual species, and with the eigen values (significant correlations in bold)

Species	PC 1	R	p	PC 2	r	p
A. custodiens	0.143	0.143	0.088	**0.676**	**0.676**	**0.000**
A. rotundatus	0.151	0.151	0.071	-0.081	-0.081	0.334
C. irredux	-0.113	-0.113	0.178	**-0.197**	**-0.197**	**0.018**
C. liengmei	0.109	0.109	0.194	-0.085	-0.085	0.313
***Camponotus* sp.**	**0.255**	**0.255**	**0.002**	**-0.203**	**-0.204**	**0.014**
D. helvolus	**0.389**	**0.389**	**0.000**	**-0.465**	**-0.465**	**0.000**
L. attenuata	-0.291	-0.029	0.730	**-0.318**	**-0.318**	**0.000**
L. castanea	0.015	0.015	0.858	**-0.390**	**-0.390**	**0.000**
L. incisa	**0.619**	**0.619**	**0.000**	**0.337**	**0.337**	**0.000**
M. capensis	**0.316**	**0.316**	**0.000**	**-0.278**	**-0.278**	**0.001**
M. opacior	**0.677**	**0.677**	**0.000**	**-0.210**	**-0.210**	**0.011**
***Monomorium* sp.**	**0.702**	**0.702**	**0.000**	-0.007	-0.007	0.933
P. megacephala	**0.220**	**0.220**	**0.008**	**0.416**	**0.416**	**0.000**
P. mandibularis	-0.002	-0.002	0.981	**0.191**	**0.191**	**0.022**
T. mossamedense	**0.551**	**0.551**	**0.000**	0.114	0.114	0.175
***Technomyrmex* sp.**	0.009	0.009	0.913	**0.535**	**0.534**	**0.000**
Eigen value	2.072			1.763		

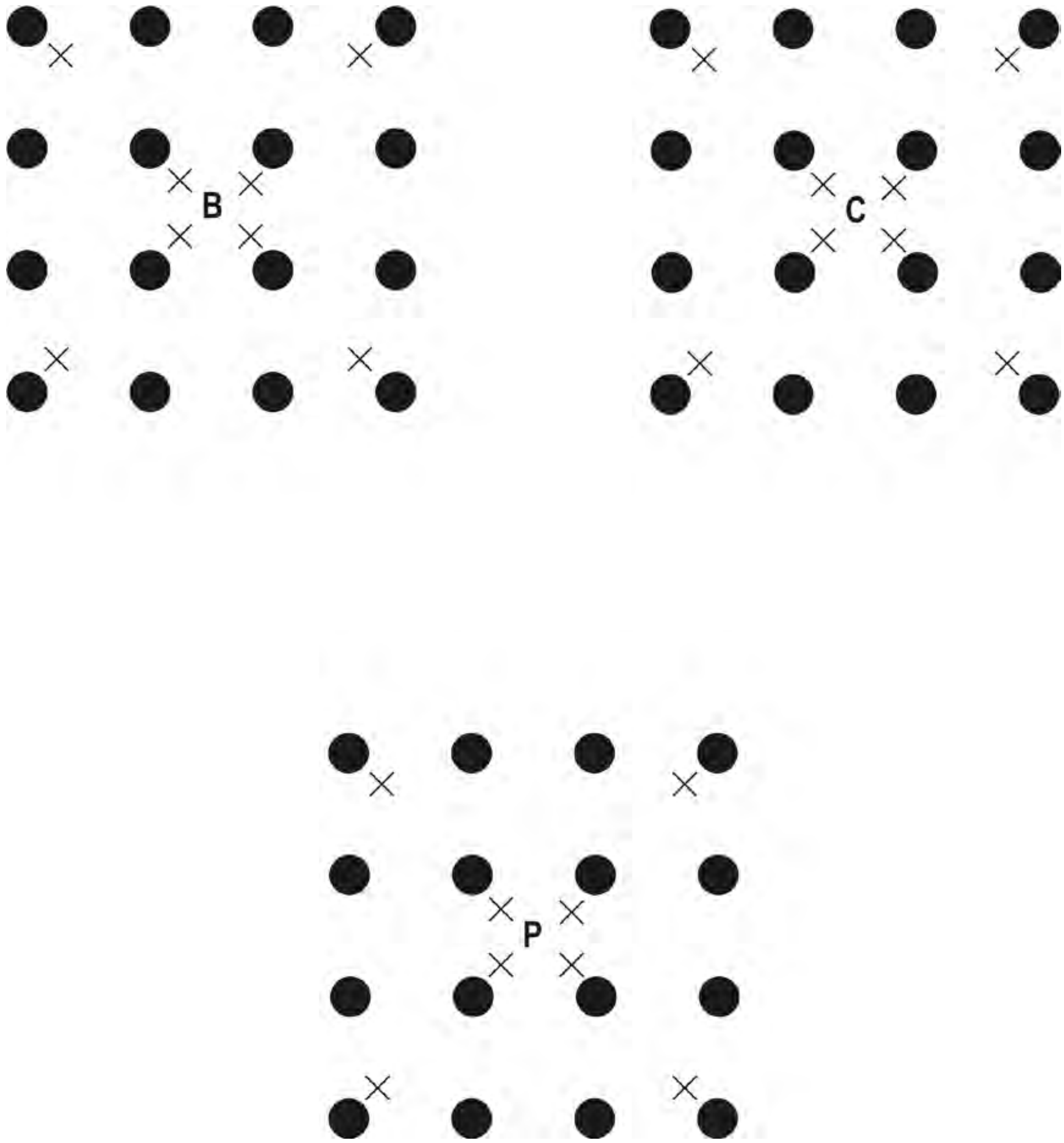

Fig. 2.1 Diagram illustrating the layout of the pitfall traps in each subunit (● trees; **x** pitfall traps; **b** banded; **c** control; **p** poisoned)

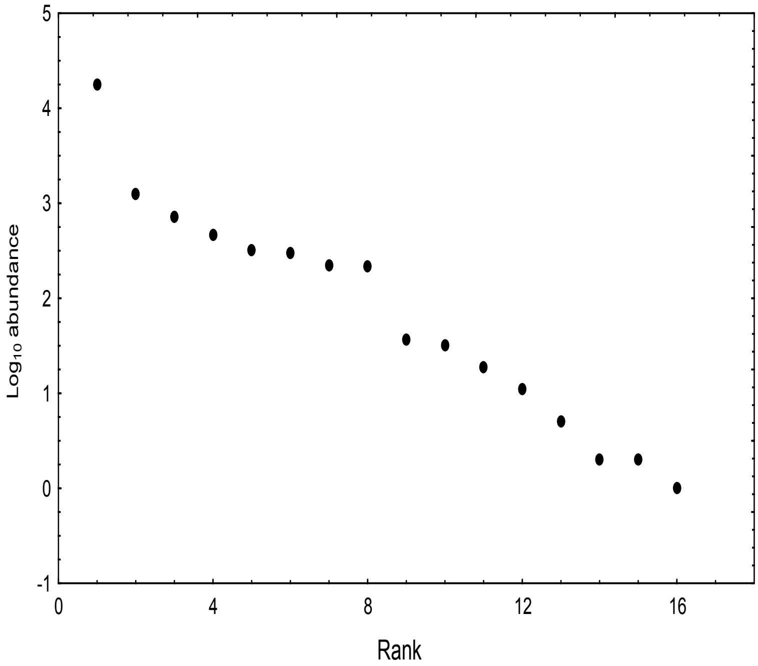

Fig. 2.2 Rank-abundance curve for ant species collected by pitfall trapping in all experimental plots at Mosslands Farm (December 2000 – April 2001 and November 2001)

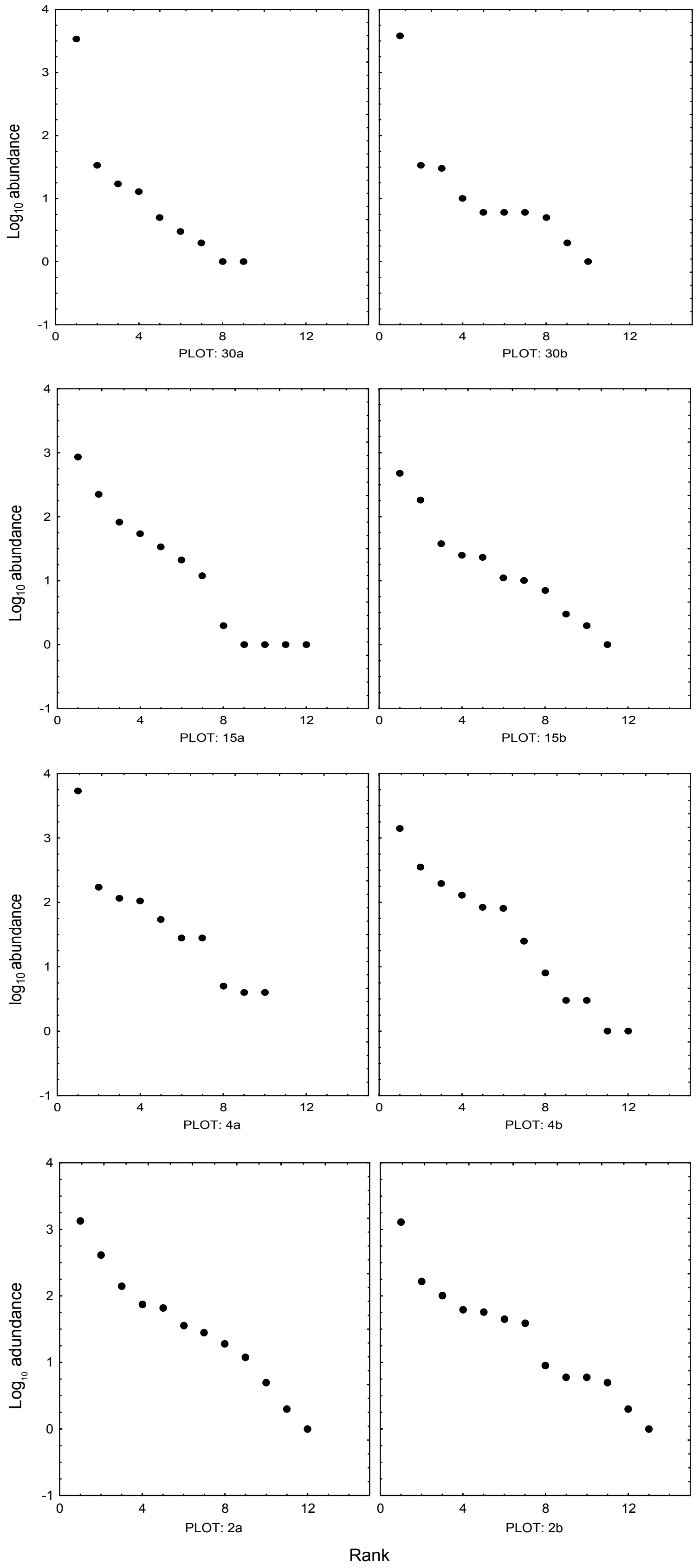

Fig. 2.3 Rank-abundance sequences for ant species in the different aged plots, measured by pitfall trapping at Mosslands Farm (December 2000 – April 2001 and November 2001)

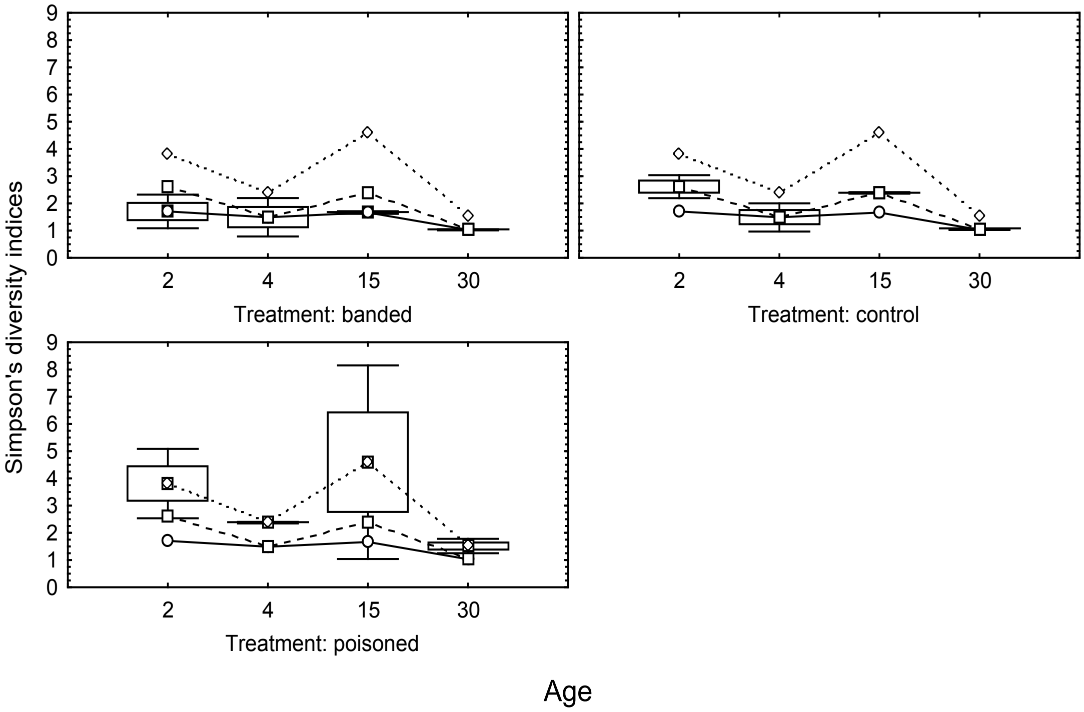

Fig. 2.4 Simpson's diversity indices for the ant communities sampled by pitfall trapping in the banded, control and poisoned subunits of the different aged plots at Mosslands Farm (December 2000 – April 2001 and November 2001) (95% CI for the mean; ○ banded, □ control, ◊ poisoned)

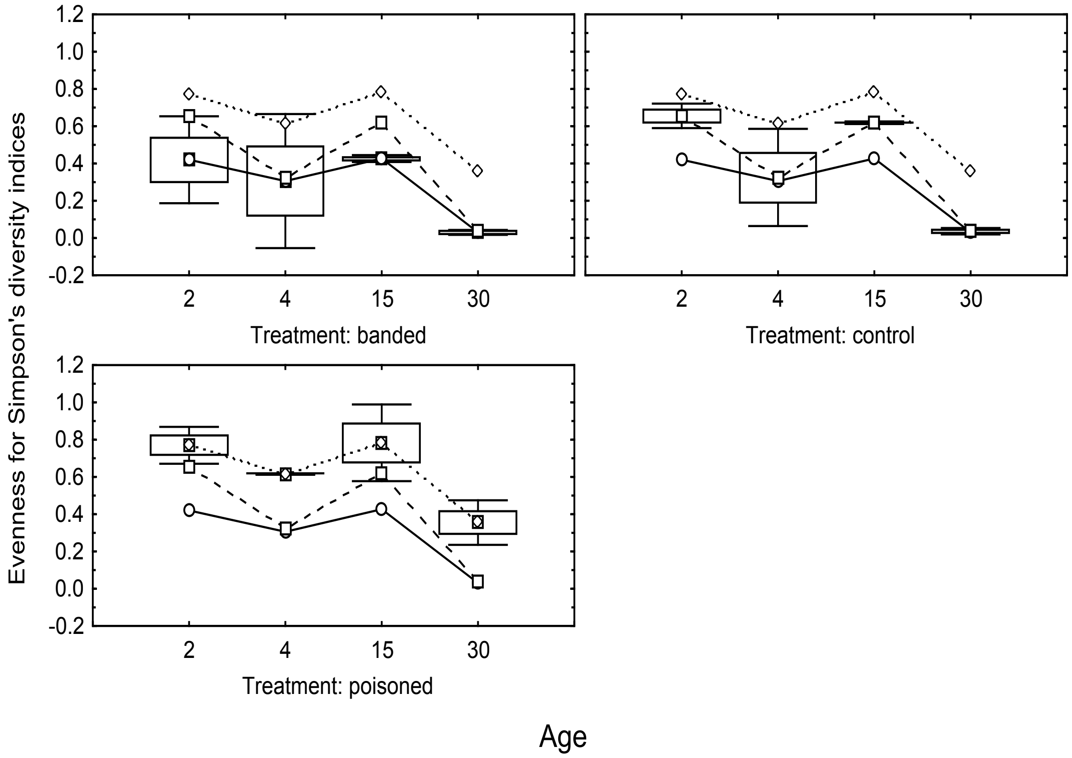

Fig. 2.5 Evenness measures from Simpson's diversity indices for the ant communities sampled by pitfall trapping in the banded, control and poisoned subunits of the different aged plots at Mosslands Farm (December 2000 – April 2001 and November 2001) (95% CI for the mean; ○ banded, □ control, ◊ poisoned)

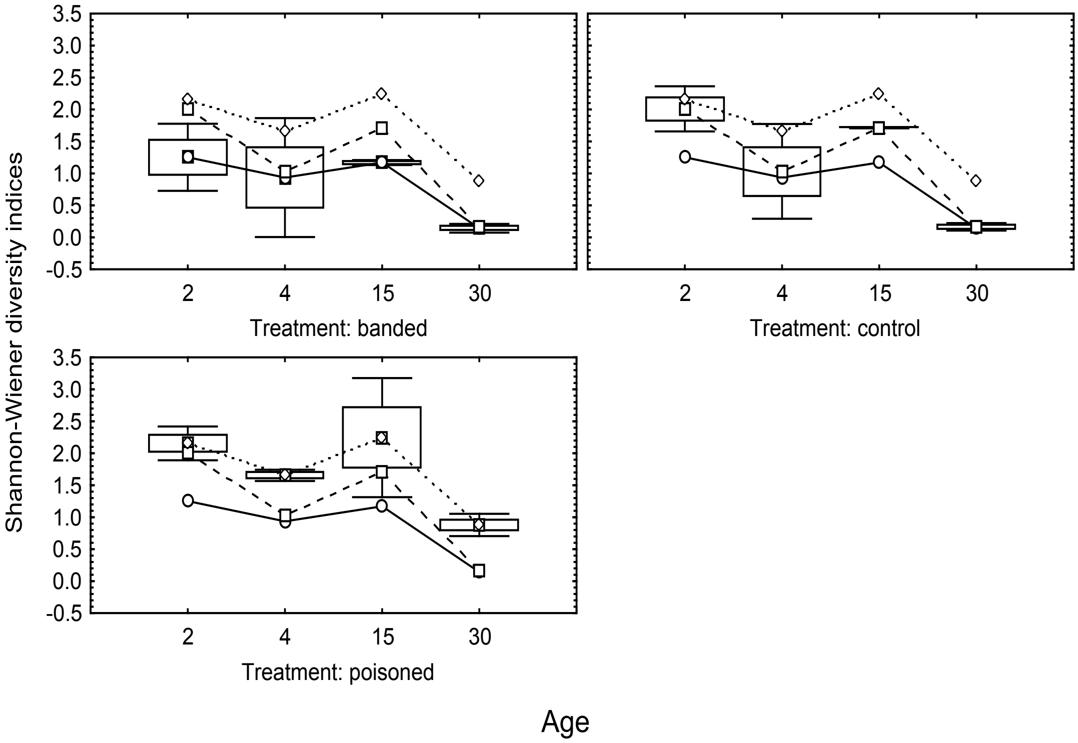

Fig. 2.6 Shannon-Wiener diversity indices for the ant communities sampled by pitfall trapping in the banded, control and poisoned subunits of the different aged plots at Mosslands Farm (December 2000 – April 2001 and November 2001) (95% CI for the mean; ○ banded, □ control, ◊ poisoned)

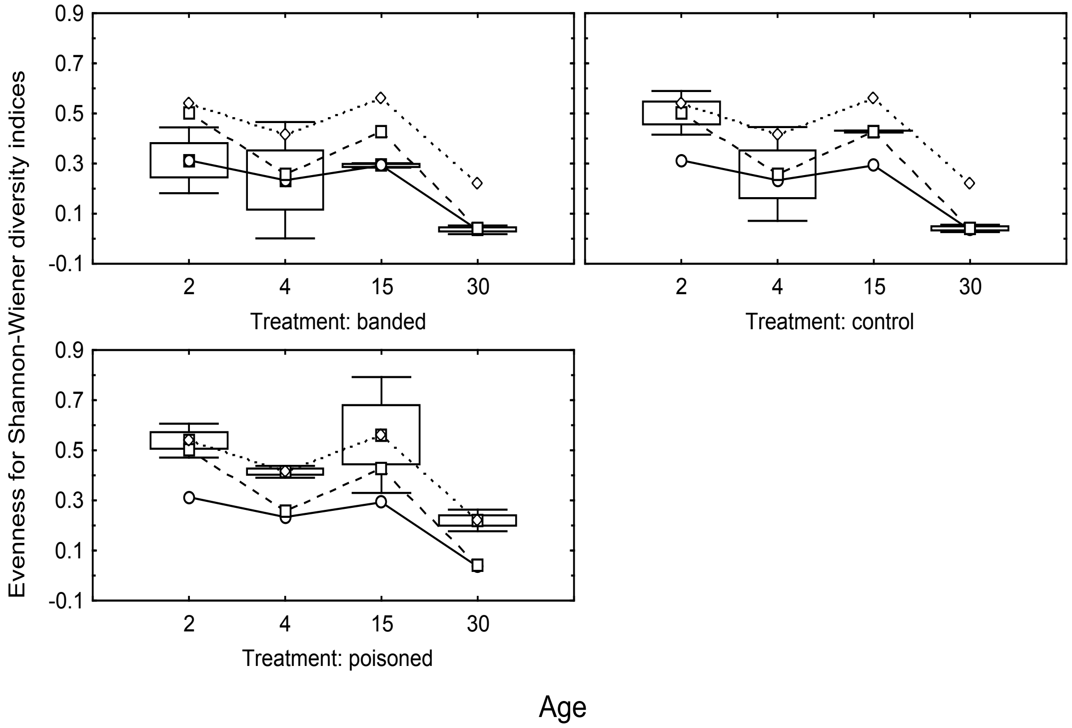

Fig. 2.7 Evenness measures from the Shannon-Wiener diversity indices for the ant communities sampled by pitfall trapping in the banded, control and poisoned subunits of the different aged plots at Mosslands Farm (December 2000 – April 2001 and November 2001) (95% CI for the mean; ○ banded, □ control, ◊ poisoned)

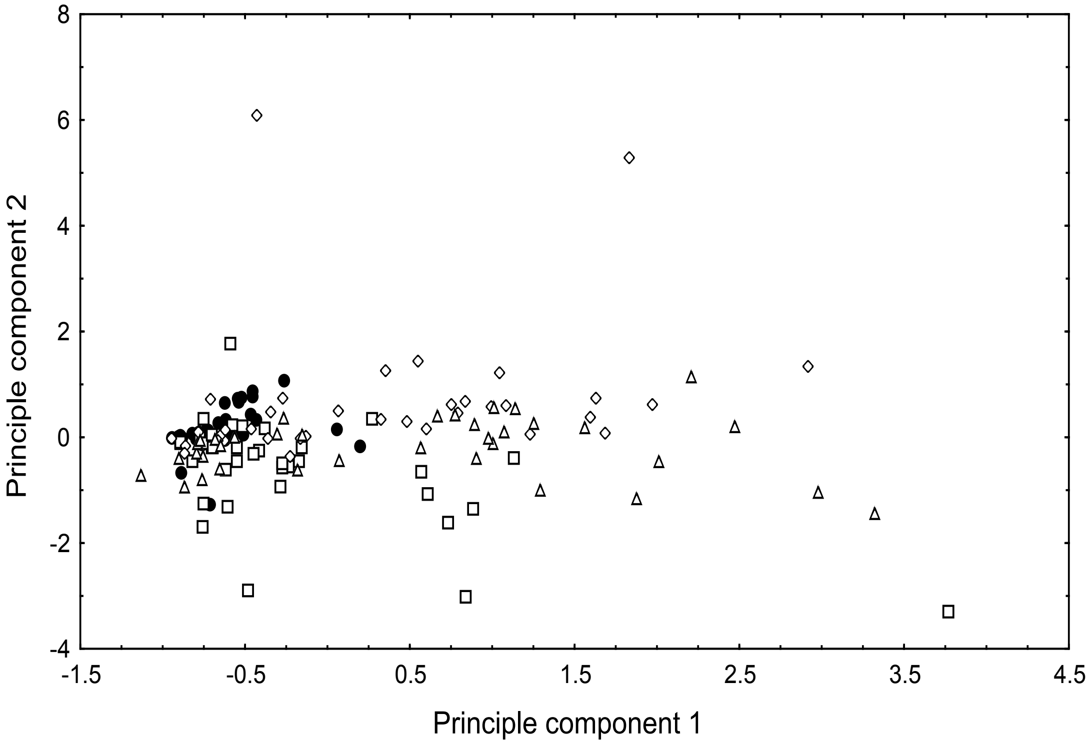

Fig. 2.8 Scatter diagram of the first two axes of a principle component analysis of the ant communities sampled by pitfall trapping at Mosslands Farm in the 2- (Δ), 4- (◊), 15- (□) and 30-year-old (●) plots (December 2000 – April 2001 and November 2001)

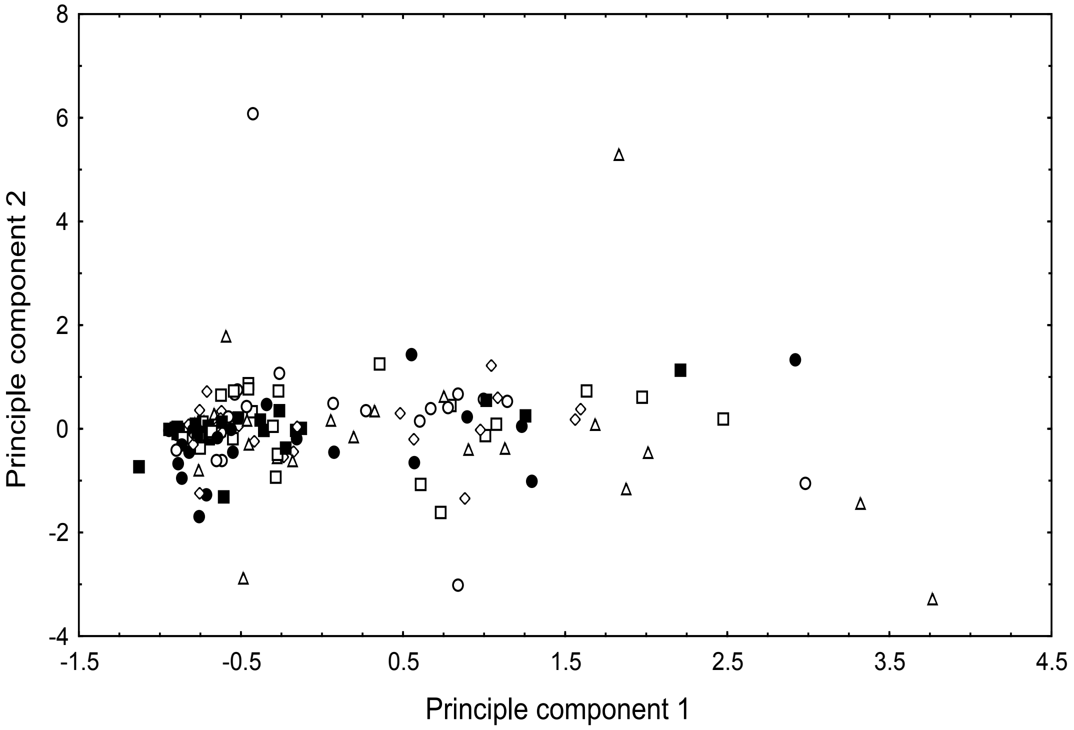

Fig. 2.9 Scatter diagram of the first two axes of a principle component analysis of the ant communities sampled by pitfall trapping at Mosslands Farm in the months December (○), January (□), February (◊), March (Δ), April (●) and November (■)

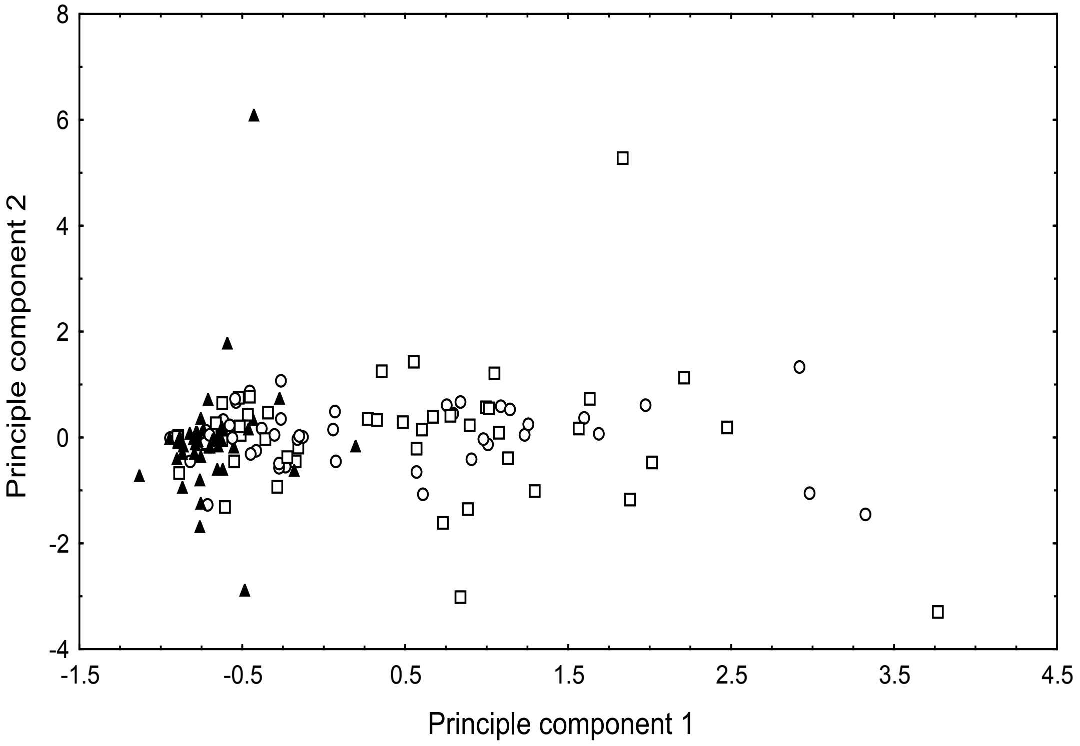

Fig. 2.10 Scatter diagram of the first two axes of a principle component analysis of the ant communities sampled by pitfall trapping at Mosslands Farm in the banded (○), control (□) and poisoned (Δ) subunits (December 2000 – April 2001 and November 2001)

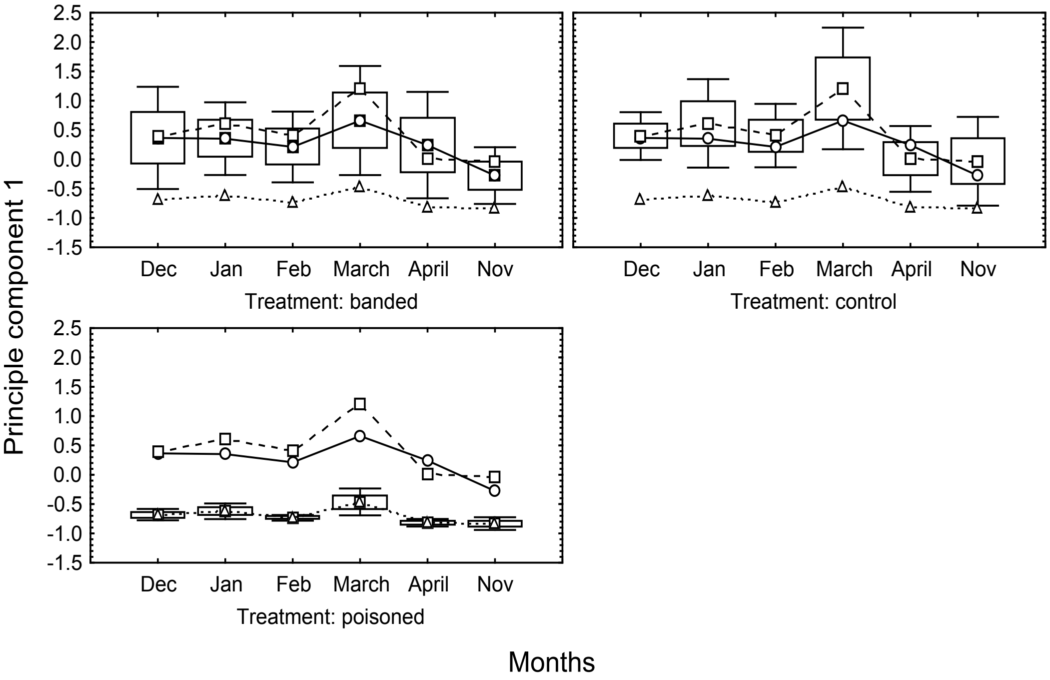

Fig. 2.11 Factor scores of the first principle component from a principle component analysis of the ant communities sampled by pitfall trapping in the banded, control and poisoned subunits during the different months at Mosslands Farm (95% CI for the mean; ○ banded, □ control, Δ poisoned)

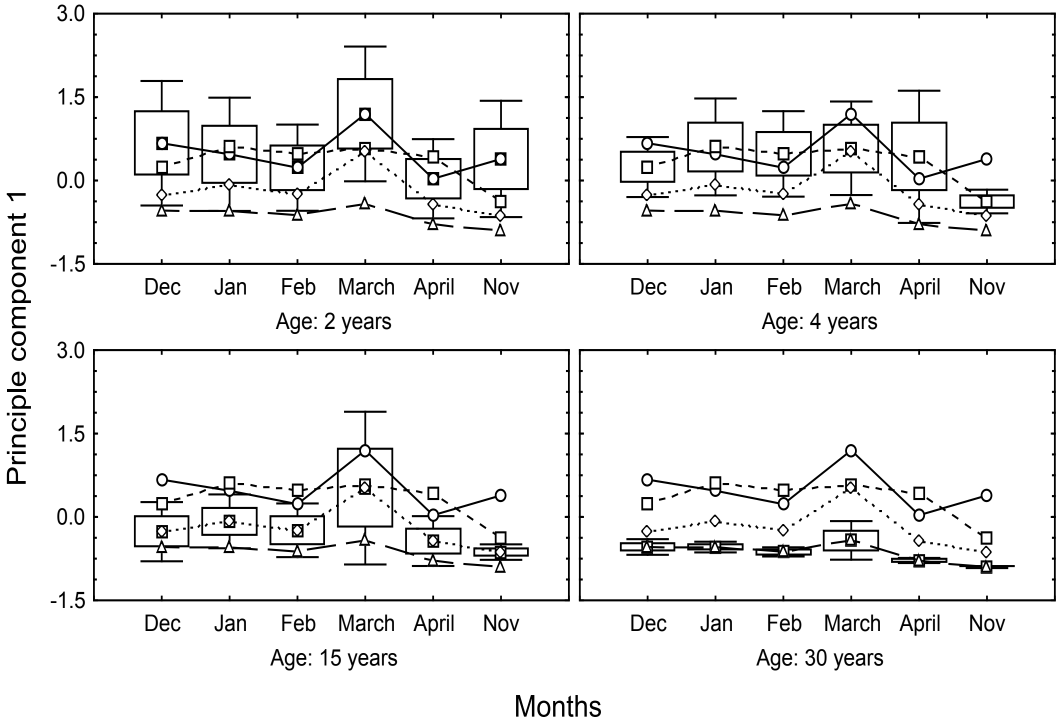

Figure 2.12 Factor scores of the first principle component from a principle component analysis of the ant communities sampled by pitfall trapping in the 2- (○), 4- (□), 15- (◊) and 30-year-old (Δ) plots during the different months at Mosslands Farm (95% CI for the mean)

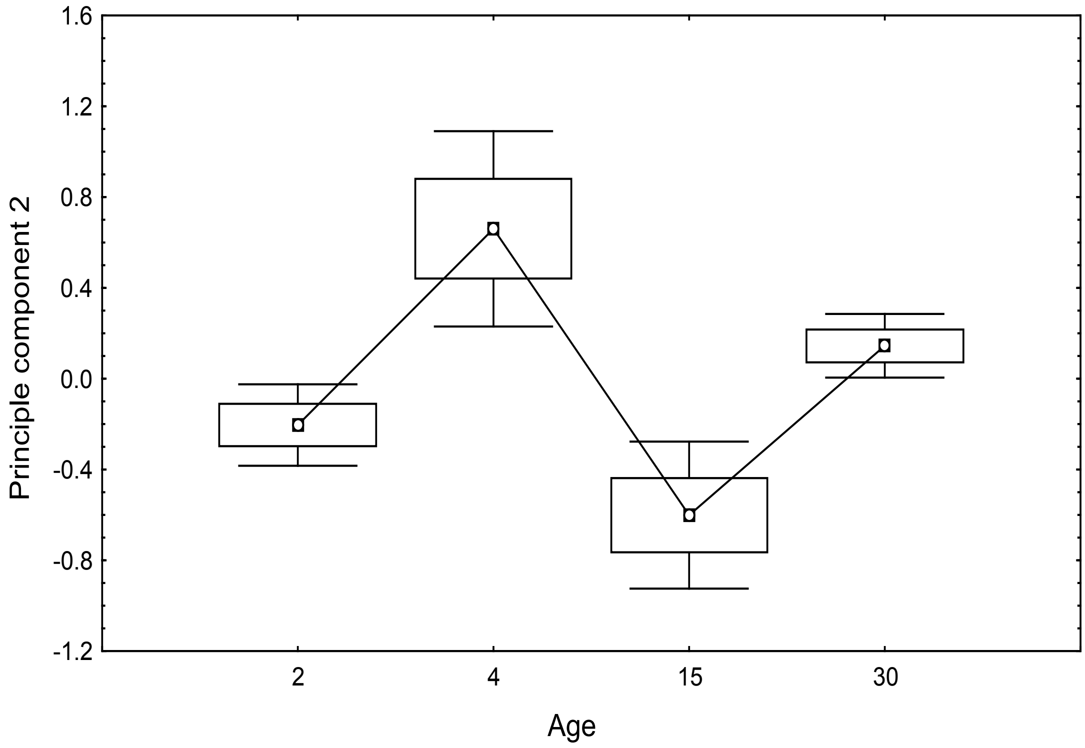

Figure 2.13 Factor scores of the second principle component from a principle component analysis of the ant communities sampled by pitfall trapping in the different aged plots at Mosslands Farm (December 2000 - April 2001 and November 2001)

3

Predation on bollworm, false codling moth and Mediterranean fruit fly pupae in citrus orchards

Summary

Bait pupae of bollworm, false codling moth (FCM) and fruit fly were exposed in bait trays in two treated subunits and a control subunit in citrus orchards of four different ages. The ages of the trees at the start of the study were 2, 4, 15 and 30 years old. In one of the treated subunits in each orchard, the trees were banded so that ants were prevented from entering the trees and in the second treated subunit, two ant species, *Pheidole megacephala* (Fabricius) and *Anoplolepis custodiens* (Smith) were poisoned. Three predation trials were conducted for bollworm and FCM and two trials were conducted for fruit fly. The duration of the trials depended on the duration of the pupal stage of each pest species. The presence of *P. megecaphala* was significantly negatively correlated ($r_s = -0.292680$; $p < 0.001$) with pest pupal survival. Survival of the pupae was significantly higher for bollworm ($p < 0.001$), FCM ($p < 0.001$) and fruit fly ($p < 0.001$) where the ants had been poisoned than in the control subunits or where the trees were banded. There was a general trend for survivorship to increase with an increase in the age of the trees. A significant difference ($p < 0.001$) was found between the months in which the trials were carried out and pupal survival was significantly lower ($p < 0.001$) for FCM than for bollworm and fruit fly. *Pheidole megacephala* can be a valuable agent in the natural control of soil-pupating citrus pests. Ant bands, rather than poisoning, are recommended as a method of ant control.

3.1 Introduction

Ants (Hymenoptera: Formicidae) are a major component of the citrus orchard fauna (Samways *et al.*, 1982) and it is well known that they can be serious indirect pests of citrus (Ullyett, 1938; Flanders, 1945; Annecke, 1958) and of other crops such as tea (Das, 1959), guavas (Samways, 1983a), pineapples (Petty, 1993) and coffee (Reimer *et al.*, 1993). Certain tree-foraging species feed on honeydew excreted by homopterous pests such as aphids, soft scales and mealybugs. The ants' activity in the trees disturbs the natural enemies of these honeydew-producing homopterans (Wheeler, 1910; Nixon, 1951; Way, 1963; Samways, 1983a), preventing them from maintaining pest populations at commercially acceptable levels. Outbreaks or epidemics of other serious pests, particularly red scale, *Aonidiella aurantii* Maskell are an indirect result of this breakdown in natural control (Steyn, 1954a, b; Bedford, 1968). Two species in particular, *Pheidole megacephala* (Fabricius) and *Anoplolepis custodiens* (Smith), which are both abundant and widespread in South African citrus production areas, are responsible for these pest outbreaks and are by far the most economically important ants (Samways *et al*, 1982; 1998).

Since the development of organophosphate resistance in red scale (Georgala, 1975; Nel *et al.*, 1979) and with the vast array of beneficial insects that are associated with citrus in South Africa (Annecke & Moran, 1982), increasing emphasis has been placed on the biological control of citrus pests (Bedford, 1998b). An IPM approach is now widely used by commercial citrus farmers whereby chemical treatments are used together with natural enemies against the pest complex. An essential factor in the success of this approach to pest control is the control of ants in citrus trees (DeBach *et al.*, 1951a; Annecke, 1963; Bedford, 1968).

As a result of their abundance, feeding habits, high diversity and their stability as populations, ants have a significant influence in many habitats (Wilson, 1971; Carroll & Janzen, 1973; Risch & Carroll, 1982a; Gotwald, 1986; Hölldobler & Wilson, 1990). As a group, they are highly predacious, playing a critical role as predators of pests in many crop systems (Way, 1951, 1953; Brown, 1959; Negm & Hensley, 1969; Greenslade, 1971; Bateman, 1972; Leston, 1973; Risch, 1981; Risch & Carroll, 1982a, b; Wong *et al.*, 1984; Watmough & Kfir, 1995; Daane & Dlott, 1998). *Anoplolepis custodiens* and

P.megacephala are effective predators of crop pests in agroecosystems. Coconut production in Tanzania benefitted from the presence of *A. custodiens* (Löhr, 1992) and the impact of *P. megacephala* in Hawaiian pineapple fields is considered to be beneficial, despite the fact that it attacks beneficial insects and tends homopterous pests (Phillips, 1934 *cited in* Gotwald, 1986). The attributes possessed by ants that are associated with the potential to act as effective biological control agents have been summarized by Risch & Carroll (1982a). They are that ants are extremely responsive to spatial variations in their food; ants can persist as viable predators in spite of temporal fluctuations in their food supply; predator satiation is not likely to limit the effectiveness of ants; ants can have a negative impact on their prey beyond that resulting from direct predation alone; and the foraging patterns of ants can be manipulated and managed in order to maximise their contact with pests. Other useful attributes are that ants are extremely diverse and abundant in tropical and temperate ecosystems and that most are predacious (Majer, 1986).

Samways (1982) and Steyn (1954a, b) have noted the beneficial effects of *A. custodiens* and *P. megacephala* in preying on larvae of citrus pests such as fruit fly, bollworm and false codling moth when they drop to the soil to pupate. However, the extent to which they control pest species has not previously been quantified.

Samways (1990a) has stressed that the principle of ant control in subtropical fruit trees must be to break the mutualism between ground-nesting ants and the tree-dwelling honeydew-producers. Chemical control measures need to be applied regularly to eradicate local ant populations and are therefore not economically feasible and are environmentally disruptive (Samways, 1990a). In addition to this, a control method, that does not completely eradicate the ants, is desirable so that they are left to prey on pest species that pupate in the soil (Samways, 1982, 1990a; Samways *et al.*, 1981). An effective, long-lasting, non-phytotoxic ant band (Ant-Bar 1.2.3), which acts as a physical barrier, preventing ants from entering the trees, has been recommended by Samways & Buitendag (1986).

If *A. custodiens* and *P. megacephala* can be shown to be important predators of soil-pupating pests in citrus orchards, the use of ant bands as opposed to poisons as a method of ant control will be strongly justified. Crop management strategies also tend to overlook the possibility of using these naturally occurring, abundant species as biological control agents in citrus orchards. The use of ant bands in guava plantations has been suggested as an ecologically sensible method of ant control (Samways, 1982). Its use in other tree crops in southern Africa, where ants are problematic in precipitating outbreaks of homopterous pests, may also prove to be beneficial.

3.2 Materials and Methods

Eight experimental plots (orchards) were chosen on Mosslands Farm (33°24 ′S 26°26′E), which lies approximately 20 km west of Grahamstown in the Eastern Cape, South Africa. All plots were navel trees. Two plots with trees of each of the ages 2, 4, 15 and 30 years old (Table 1.1) were selected from those available throughout the farm (Fig. 1.1).

Within each of these plots, three non-overlapping subunits, each consisting of a square of 16 trees (Fig. 2.1), served as individual sampling sites and were each assigned to one of three different treatments. In one subunit, ants were excluded from the trees using the ant band, ‘Ant Bar 1.2.3.’(supplied by KatCo). This band, recommended by Samways and Buitendag (1986), is a highly effective method of keeping ants out of the trees (Samways, 1990a). The bands, consisting of a layer of bidim or polyester fibre held in place by two to three layers of stretch wrap plastic, were placed halfway up the trunks of the trees. A third layer of Plantex, a polybutene and wax compound that remains sticky for several months, which acts as a sticky barrier, was applied on top of the plastic. It was effective in preventing ants from entering the trees. Ant bands were checked regularly and the Plantex reapplied if necessary and tree skirtings and weed bridges that may have provided the ants with an alternative route up the tree were removed (Samways, 1990a). In a second subunit, colonies of *P. megacephala* were poisoned so that their populations were significantly depressed. This was done using Amdro (Hydramethylnon ant-bait), which was applied at 0.2 g per square metre. Amdro is a proprietary bait that was developed for the control of the fire ant *Solenopsis invicta* Buren in the USA and which is effective in suppressing *P. megacephala* (Samways, 1985; Petty, 1993). The application rate used, was recommended by Petty (1993; pers. comm.) who found it to be effective at this dosage. Reinvasion of this species was monitored by pitfall trapping and the treatment reapplied when necessary. Populations of *A. custodiens* were poisoned with parathion, which was sprayed into their nest entrances at a dosage of 7ml per litre of water, on the advice of the farm owner, Rob Moss (pers. comm.). This is lower than the recommended concentration but the grower claimed to have achieved satisfactory results with the applied concentration. A third subunit in each plot served as an untreated control in which the trees were not banded and ants were not poisoned. During the trials, ant community structure in the experimental subunits was monitored by pitfall trapping. Trapping was done for a period of five days. For a description of the pitfall traps, refer to section 2.2. The ants were collected from the pitfall traps in the laboratory and identified to genus and where possible, species using Arnold's (1915) monograph of the southern African Formicidae. Voucher specimens were sent to the South African Museum for confirmation of the identifications, and are now held there as part of the reference collection.

Predation on soil-pupating pests was quantified by planting bait pupae of bollworm, false codling moth and Mediterranean fruit fly in bait trays in all the subunits. Two bait trays, which consisted of a flowerpot drip tray buried in the soil to a depth of approximately 3 cm, were placed on the northern and southern sides of the inner four trees in each subunit. A plastic flowerpot was placed upside down over the bait trays. A hole about 5 cm in diameter was made in the base of the flowerpot and a plastic bag stuck over the top in order to trap adults that successfully emerged. Sections of the rim of the flowerpot were cut away to allow for the movement of ants in and out of the pots and therefore access to the bait trays. This trap was modified from a blowfly-collecting trap (Erzinçlioğlu, 1995). During a trial, six to eight pupae were placed in each of these trays and covered with a layer of soil. Three trials were conducted with bollworm and FCM pupae and two trials were conducted with fruit fly pupae. The duration of the trial depended on duration of the pupal stage of each species. The pupal stage lasts for 15.5 days in bollworm (Vermeulen & Bedford, 1998), 10 to 15 days in fruit fly (Du Toit, 1998) and for FCM the duration of the pupal stage is given as 21 to 24 days in summer and 29 to 40 days in winter (Newton, 1998). In order to count the number of pupae that successfully eclosed i.e. that were not preyed upon during the trials, the number of whole pupal cases left at the end of each trial were counted. These were distinguishable from those that had been eaten as they were split along the hatching lines, signifying eclosion. These have been called "survivors". The pest species and the number of pupae that were planted in each bait tray during a trial and the month of the year in which the trials were carried out are given in Table 3.1.

Because the number of pupae planted in the bait trays for the bollworm trials differed between the trials and the bait trays, the number of survivors had to be transformed into proportions before statistical analysis. This was done using the arcsine transformation for all of the species. A multi-way ANOVA (Zar, 1974) was used to analyse the effect of age and treatment on the number of survivors. Tukey's honestly significant difference (HSD) test for an unequal sample size (N) (Spjotvoll/Stoline test) was used for a post hoc comparison of the means for the bollworm trials. Tukey's HSD test was used for a post hoc comparison of the means for the FCM and fruit fly trials. For analysis of the effect of the time of year and treatment on the proportion of surviving pupae, a multi-way ANOVA was used. Tukey's HSD test for an unequal sample size (N) (Spjotvoll/Stolline test) was used for a post hoc comparison of the means. Survivorship was correlated with the presence and the relative abundance of the ant species using Spearman's rank order correlation analysis. A one-way ANOVA (Zar, 1974) was used to test for the significance of these correlations. All statistics tests were done in Statistica, version 5.5.

3.3 Results

A significant difference (bollworm: $F = 6.199$, $p < 0.001$; FCM: $F = 17.194$, $p < 0.001$; fruit fly: $F = 18.543$ $p < 0.001$) in the proportion of surviving pupae of each pest species was found between the poisoned subunits and the banded and control subunits, but no significant difference was found between the banded and control subunits (Figs. 3.1 – 3.3; Tables 3.2 – 3.4).

Bollworm

There was a significant ($F = 9.111$; $p < 0.001$) general trend for the proportion of survivors to decrease with an increase in the age of the trees. The interaction between age and treatment is significant ($F = 3.308$, $p < 0.001$). The proportion of pupae that survived was significantly higher in the poisoned subunits of the plots with trees aged 15 years old (plots 15a and 15b) than in the banded and control subunits (Fig. 3.1; Table 3.2). The proportion of survivors was higher in the poisoned subunits of the plots with trees aged 4 (plots 4a and 4b) and 30 (plots 3a and 30b) years old, and lower in the poisoned subunits of plots with 2-year-old trees (plots 2a and 2b), but these differences were not statistically significant (Fig. 3.1; Table 3.2).

False codling moth

There was a significant general trend for the proportion of surviving pupae to increase with an increase in the age of the trees, but this was not statistically significant (Fig. 3.2; Table 3.3). The interaction between age and treatment was not significant. The proportion of pupae that survived was higher in the poisoned subunits of the plots with trees aged 2 (plots 2a and 2b), 15 (plots 15a and 15b) and 30 (plots 30a and 30b) years old than in the banded and control subunits (Fig. 3.2; Table 3.3).

Fruit fly

There was a significant general trend for the proportion of survivors to increase with an increase in the age of the trees (Fig, 3.3; Table 3.4). The interaction between age and treatment was not significant. Tukey's HSD test produced four homogenous groups (Table 3.4). Survivorship was similar and highest in the banded and poisoned subunits of the plots with 30-year-old trees (plots 30a and 30b) and in the poisoned subunits of the plots with 15-year-old trees (plots 15 and 15b) (Fig. 3.3; Table 3.4).

The proportion of pupae that survived was significantly higher ($F = 35.010$; $p < 0.001$) in the poisoned subunits than in the banded and control subunits during all the months in which the trials were carried out (Fig. 3.4). There was a significant difference ($F = 21.092$; $p < 0.001$) in the proportion of survivors between the months in which the trials were carried out. Survivorship was significantly lower in March, April and May 2001 than in December 2000, January, February, October and November 2001. The interaction between age and treatment was not significant. Survivorship was significantly lower ($F = 30.286$; $p < 0.001$) for FCM than for bollworm and fruit fly (Table 3.5).

Significant negative correlations were found between survivorship and the presence and relative abundance of *P. megacephala* ($r = -0.293$; $p < 0.001$), *Monomorium* sp. ($r = -0.199$; $p = 0.017$) and *Technomyrmex* sp. ($r = -0.169$; $p = 0.048$) (Table 3.6).

3.4 Discussion

Pheidole megacephala was extremely abundant and was the exclusive dominant ant in all of the plots (Table 2.2), thus it is likely that this species would have played a more critical role as a predator during the trials than other predatory or scavenger ant species. Pest pupal survival was significantly negatively correlated with the presence of *P. megacephala* and, although the results were variable, the numbers of bait pupae that reached eclosion during the trials were mostly higher where populations of *P. megacephala* had been suppressed. Thus the presence of *P. megacephala* had a negative impact on the survival of the pupae, and predation on the pupae was less efficient at significantly low population levels of this species. When bait traps were checked two to three days after pupae had been planted, they were often swarming with *P. megacephala* workers. These results and observations strongly suggest that *P. megacephala* preys on soil-pupating citrus pests and thus plays a role in biological control.

Predation on pupae in the banded and control subunits was similar during all of the trials, thus it seems that regardless of whether the ants have access to the trees or not, their foraging patterns on the ground are the same.

Predation on FCM and fruit fly pupae was heavier than on bollworm. This could be due to the large size of bollworm pupae, which are 13.5 to 18 mm in length (Du Toit, 1998) as opposed to 4 to 6 mm for fruit fly (Vermeulen & Bedford, 1998) and 6 to 7 mm for FCM (Gunn, 1921). *Pheidole* spp. tend to prey on smaller prey items such as nematodes, fruit maggots, root maggots and rootworm eggs (Gotwald, 1986; Risch, 1981). *Pheidole megacephala*, and the predator complex as a whole, may therefore have been less efficient at preying on larger bollworm pupae.

It is also possible that the duration of the pupal stage of each species and the rate of development of the pupae had an influence. The duration of the pupal stage of FCM, which had the lowest survivorship, is the longest of the three species. Pupal development in FCM takes 21 to 24 days in summer and 29 to 40 days in winter (Newton, 1998). The pupal stage of fruit fly is 10 to 15 days (Du Toit, 1998) and bollworm's pupal stage is 15.5 days (Vermeulen & Bedford, 1998). The development rate of the egg, larval and pupal stages of all insects is largely dependant on temperature. The development rate increases with an increase in temperature. In terms of the effect of temperature on the development rate of the pupae during the trials, FCM would have, comparatively, had the slowest development of the three species due to the time of year in which the trials were carried out. The fruit fly and bollworm trials were conducted during spring and summer, whereas the FCM trials were conducted during Autumn, when temperatures would have been cooler. The longer the development period of the pupae, the more time predators have to find them before eclosion. Soil predators may be more efficient when the development rate of pests is slower. They may also have a particularly significant impact on winter pests or those that are overwintering in the soil.

In the poisoned subunits, pupal survival was still low, therefore other soil predators, eg. *Dorylus helvolus*, inflicted heavy mortality on the pupae, and thus also play a significant role in the control of soil-pupating pests. Pupae were apparently preyed upon by spiders belonging to the genus *Latrodectus*. Spiders constructed their webs inside of the flowerpots and collected pupae from the bait trays and spun them into their webs. Spiders are one of the most abundant predator groups in agro-ecosystems (Van den Berg & Dippenaar-Schoeman, 1991) and are present throughout the year (Dippenaar-Schoeman, 1979). Recent studies on spiders in citrus have shown them to be important predators of pests such as citrus psylla (Van den Berg *et al.*, 1987; 1992). It has since been suggested that spiders contribute to the control of citrus pests such as citrus thrips, fruit fly and FCM (Stephen *et al.*, pers. comm.). Ground-living spiders feed on larvae hibernating in the soil (Dippenaar-Schoeman, 1998), and thus may also be important predators of other life stages associated with the soil, such as pupae. Negm & Hensley (1967, 1969) found the importance of ant populations and spider populations as predators of the sugarcane borer to vary with locality, population density and the time of year. This demonstrates the importance of the predator complex as a whole. When ant activity is low, spiders and other predaceous arthropods may play a more critical role as predators.

Insecticide applications can result in the suppression of predatory arthropod populations (Hensley *et al.*, 1961). Pupal survival was generally higher in the old plots (30a, 30b, 15a and 15b), which had received chemical treatments for several years previous to the study. However, during the bollworm trials, pupal survival was the lowest in the 30-year-old plots, which were treated with Tokuthion and Tartox just prior to the start of the trials. It therefore seems that, as expected, these chemical applications had no effect on the predaceous arthropod fauna. The habitat in the young orchards may have been more favourable to a variety of predatory species than the old orchards. Ant community diversity was higher in the young orchards (chapter 2) therefore it seems that an ecological mix of species is more favourable for more efficient pest control.

Pheidole megacephala dominated all of the plots. Majer (1972) divided ants into four status groups: a dominant species predominates numerically to the exclusion of other dominants; dominants can co-exist under certain circumstances and are then referred to as co-dominants; subdominants can reach dominant status in the absence of dominant ants and non-dominants live within or between areas of dominant ants. The work of Room (1971), Majer (1972) and Leston (1973) on tropical tree crops in Ghana has shown that dominant ants are distributed in a mosaic pattern and that each of these dominants is a keystone species. The activities of a keystone species have an important influence in determining community structure (Paine, 1974). In the cultivation of tropical tree crops, the ant mosaic is of major importance, as many pests and plant diseases are positively or negatively associated, either directly or indirectly, with one or more dominant species (Leston, 1973; 1978). These dominants have a number of properties in common: mature colonies have thousands of workers; all dominants are broad-spectrum predators and they all tend Homoptera (Leston, 1973). Dominant ants include those species that are most often used for biological control (Way & Khoo, 1992). *Pheidole megacephala* exhibits all of the properties of dominant ants that are used in pest control in tropical tree crops. This emphasises the potential of this species to act as an effective biological control agent.

Since the elucidation of the ant mosaic in the tropics and its beneficial effects in terms of the limiting of pests and diseases associated with the crops, several studies have been done on its maintenance and manipulation to enhance beneficial species and encourage the displacement of the harmful ones (Majer, 1976a, b, c). Finnegan (1971) has listed criteria to be used for evaluating predacious ant species and Room (1973) has drawn up a step-by-step scheme for the selection and development ants as natural control agents. Methods of ant manipulation in crop systems include selective poisoning or the mechanical removal of pest-ant populations to encourage adjacent beneficial residents; the introduction of beneficials from other regions; and habitat modification (Majer, 1986). Most ant species that play an important role in pest control also tend Homoptera, thus cost-benefit judgements are needed when selecting a species as a biological control agent (Gotwald, 1986, Way & Khoo, 1992). *Pheidole megacephala* can be a major pest in citrus and other crops through precipitating outbreaks of Homoptera. However, if this species is controlled with the use of ant bands, thus preventing them from causing outbreaks of homopterous pests, their presence in orchards can only be beneficial.

Although ant manipulation has proved to be an effective method of maximising a species' efficiency in protecting tree crops from pests, the manipulation of *P. megacephala* to enhance their protective effect is not necessary. Wherever it occurs, it tends to dominate (Samways *et al.*, 1998) and is not easily outcompeted by other species. The advantage of this is obvious: a beneficial species can be used with minimal input. Rather, focus should be on the conservation of this species.

Ants are important in agroecosystems, not only in terms of their benefits as predators of pests. They move and aerate the soil, facilitate the cycling of nutrients and some may be important in pollination (Gotwald, 1986), if their metapleural gland secretions do not deactivate the pollen (Hamish Robertson, pers. comm). Thus, their elimination in crop systems could be detrimental to the maintenance of healthy and productive crops.

Pest control in recent years has gone from the incessant application of insecticides to a more ecologically based approach to pest control. The use of insecticides was originally thought to be without major disadvantages, but its increasingly disruptive impact on ecosystems over the years (Smith & van de Bosch, 1967) called for an alternative approach to pest control. Integrated Pest Management (IPM) was the concept that emerged. The term, integrated control was introduced by Stern *et al.* (1959) and was defined as "applied pest control, which combines and integrates biological and chemical control. Chemical control is used as necessary and in a manner which is least disruptive to biological control". Applying ecological principles to an IPM approach attempts to manage the agroecosystem in ways that are compatible with nature. Orchard agroecosystems provide opportunities for adopting this kind of approach to IPM as a result of their temporal and spatial stability (Brown, 1999). IPM in citrus should involve multiple tactics that are compatible. An additional focus should be that appropriate actions are taken to maintain a healthy crop, so that the focus is on crop management, rather than pest management (Hoy, 2000). The use of ant bands to control ants in citrus is compatible with an IPM approach. The ants are prevented from causing proliferation of pests that are deleterious to the crop, while playing an important role in natural pest control. Chemical control of ants is then not necessary and the need for pesticide applications should be reduced. There is thus also minimal or no risk of destroying non-target species that are beneficial in the system. Ant bands are economically feasible and are in no way harmful to the environment or beneficial organisms in the system.

Pheidole megacephala can be a valuable agent in the natural control of citrus pests. With the increasing emphasis on a more natural approach to pest control, their use can have considerable benefits in citrus and other crop systems. Although this species is a potential pest, an effective method of control is available, which eliminates their harmful effects while allowing them to play a key role in the control of soil-pupating pests in citrus. Poisoning as a control method could ultimately do more harm than good. Ants play an important role in the health and stability of ecosystems and have other benefits in crop systems in addition to pest control. Poisoning may also have a negative effect on the predator complex as a whole, which has an important influence on the development of pest populations. As a result of their abundance in orchards, *P. megacephala* has the capacity to inflict heavy predation and together with other predators in the system can have a significant impact on soil-pupating agricultural pests. The use of ant bands on other tree crops should also be considered.

Table 3.1 Pest species used and the number of pupae planted in the bait trays during each trial at Mosslands Farm and the months in which they were carried out.

Trial	Species	Date	Plots	No. of pupae
1	Bollworm	Dec 2000	1,5,6,7	6
			2,3,4,8	7
2	Bollworm	Jan 2000	1,2,6,7	6
			3,4,5,8	8
3	Bollworm	Feb 2001	2,3	6
			1,4,5,6,7,8	8
4	FCM	March 2001	All	6
5	FCM	April 2001	All	6
6	FCM	May 2001	All	6
7	fruit fly	Oct 2001	All	8
8	fruit fly	Nov 2001	All	8

Table 3.2 Post hoc comparisons of the means of the proportion of surviving pupae from the bollworm trials for the interaction between age and treatment using Tukey's honestly significant difference (HSD) test for an unequal sample size (N) (Spjotvoll/Stoline test) ($\alpha = 0.05$).

Age	Treatment	Mean	Homogenous Groups	
			1	2
30	control	0.043	x	
30	banded	0.043	x	
4	banded	0.068	x	
30	poisoned	0.100	x	
15	control	0.104	x	
4	control	0.110	x	
4	poisoned	0.120	x	
2	poisoned	0.122	x	
2	control	0.132	x	
15	banded	0.143	x	
2	banded	0.149	x	
15	poisoned	0.324		x

Table 3.3 Post hoc comparisons of the means of the proportion of surviving pupae from the false codling moth trials for the interaction between age and treatment using Tukey's honestly significant difference (HSD) test ($\alpha = 0.05$).

Age	Treatment	Mean	Homogenous Groups	
			1	2
2	banded	0.000	x	
2	control	0.000	x	
4	control	0.000	x	
4	banded	0.000	x	
15	control	0.020	x	
15	banded	0.020	x	
30	banded	0.020	x	
30	control	0.041	x	
4	poisoned	0.062	x	
15	poisoned	0.208	x	x
2	poisoned	0.208	x	x
30	poisoned	0.312		x

Table 3.4 Post hoc comparisons of the means of the proportion of surviving pupae from the fruit fly trials for the interaction between age and treatment using Tukey's honestly significant difference (HSD) test (α = 0.05).

Age	Treatment	Mean	Homogenous Groups			
			1	2	3	4
4	control	0.000	x			
2	control	0.062	x			
4	banded	0.062	x			
15	control	0.187	x	x		
2	banded	0.187	x	x		
4	poisoned	0.258	x	x		
15	banded	0.281	x	x		
2	poisoned	0.312	x	x		
30	control	0.437	x	x	x	
30	banded	0.687		x	x	X
15	poisoned	0.906			x	X
30	poisoned	1.250				X

Table 3.5 Post hoc comparisons of the means of the proportion of surviving pupae for all the trials for the effect of species on the proportion of pupae that survived using Tukey's honestly significant difference (HSD) test for an unequal sample size (N) (Spjotvoll/Stoline test) (α = 0.05).

Species	Mean	Homogenous Groups	
		1	2
FCM	0.025	x	
fruit fly	0.112		x
bollworm	0.122		x

Table 3.6 Spearman's rank order correlations and significance values for survivorship and the relative abundance of the various ant species sampled by pitfall trapping at Mosslands Farm from December 2000 to April 2001 and November 2001(significant correlations in bold).

Species	r	p-level
Monomorium opacior	-0.100	0.233
Pheidole megacephala	**-0.293**	**0.000**
Lepisiota incisa	-0.113	0.177
Camponotus sp.	-0.061	0.471
***Technomyrmex* sp.**	**-0.165**	**0.048**
***Monomorium* sp.**	**-0.199**	**0.017**
Aenictus rotundatus	-0.022	0.790
Tetramorium mossamedense	-0.147	0.079
Camponotus irredux	-0.100	0.231
Dorylus helvolus	0.084	0.315
Leptogenys attenuata	0.103	0.218
Leptogenys castanea	0.024	0.774
Anoplolepis custodiens	-0.046	0.582
Plectroctena mandibularis	-0.117	0.079
Messor capensis	-0.083	0.324
Crematogaster liengmei	-0.083	0.324

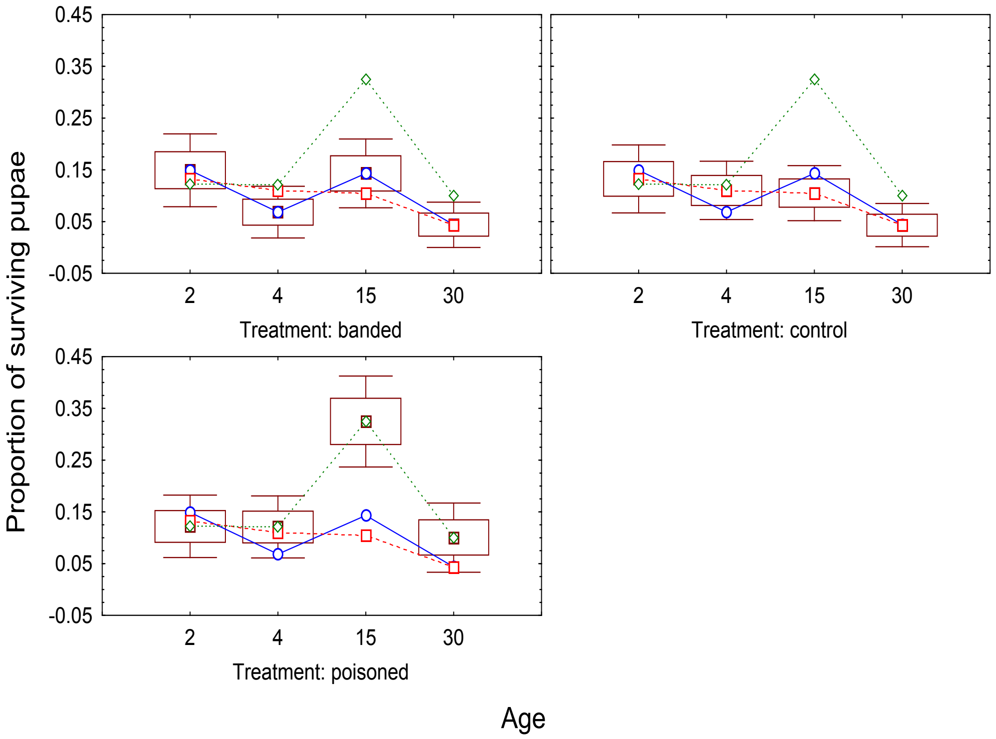

Fig. 3.1 The effect of age and treatment and their interaction on the proportion of pupae that survived during the bollworm (*Helicoverpa armigera*) trials, conducted at Mosslands Farm from December 2000 to February 2001 ($p < 0.001$; 95% CI for the mean; ○ banded, □ control, ◊ poisoned).

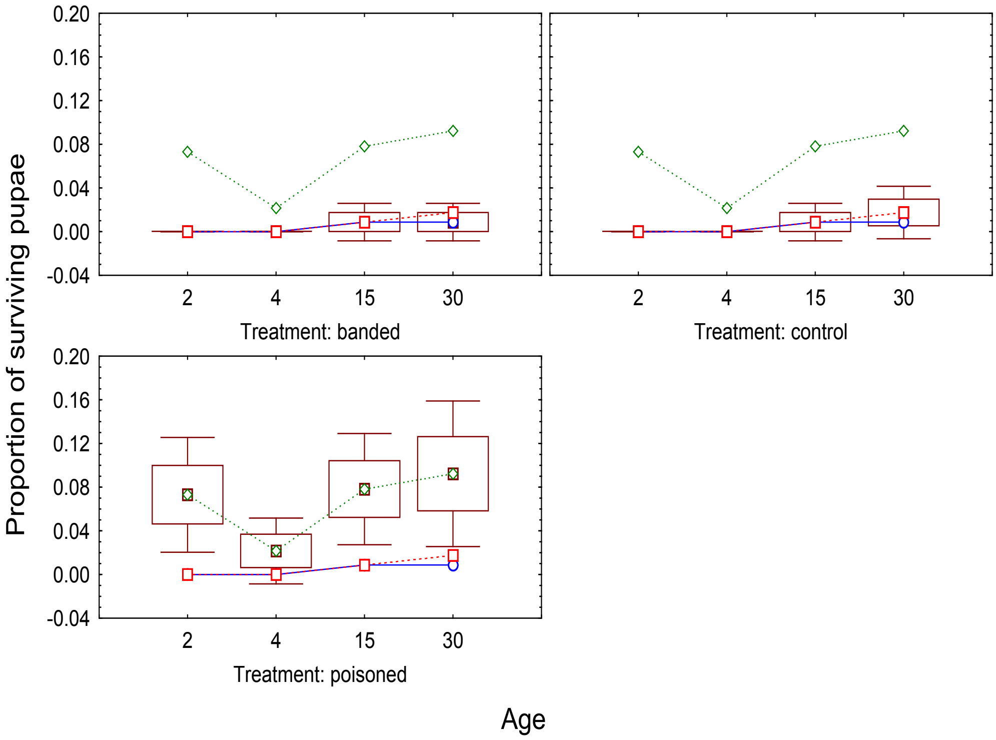

Fig. 3.2 The effect of age and treatment and their interaction on the proportion of pupae that survived during the false codling moth (*Cryptophlebia leucotreta*) trials, conducted at Mosslands Farm from March 2001 to May 2001 (95% CI for the mean; ○ banded, □ control, ◊ poisoned).

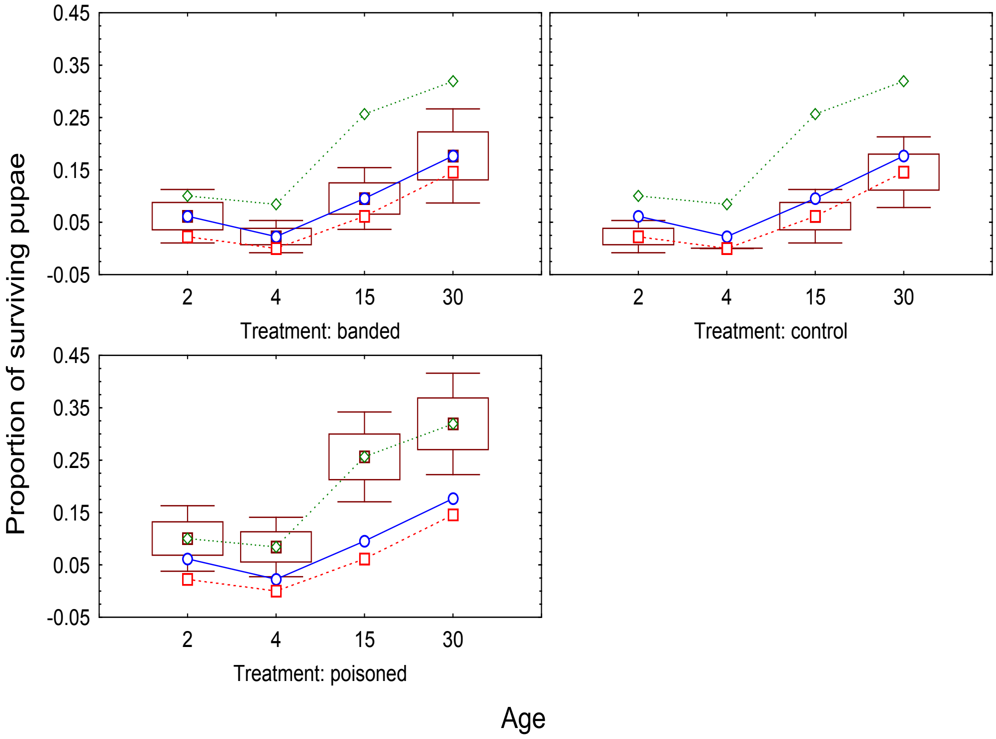

Fig. 3.3 The effect of age and treatment and their interaction on the proportion of pupae that survived during the fruit fly (*Ceratitis capitata*) trials conducted at Mosslands Farm from October 2001 to November 2001 (95% CI for the mean, ○ banded, □ control, ◊ poisoned).

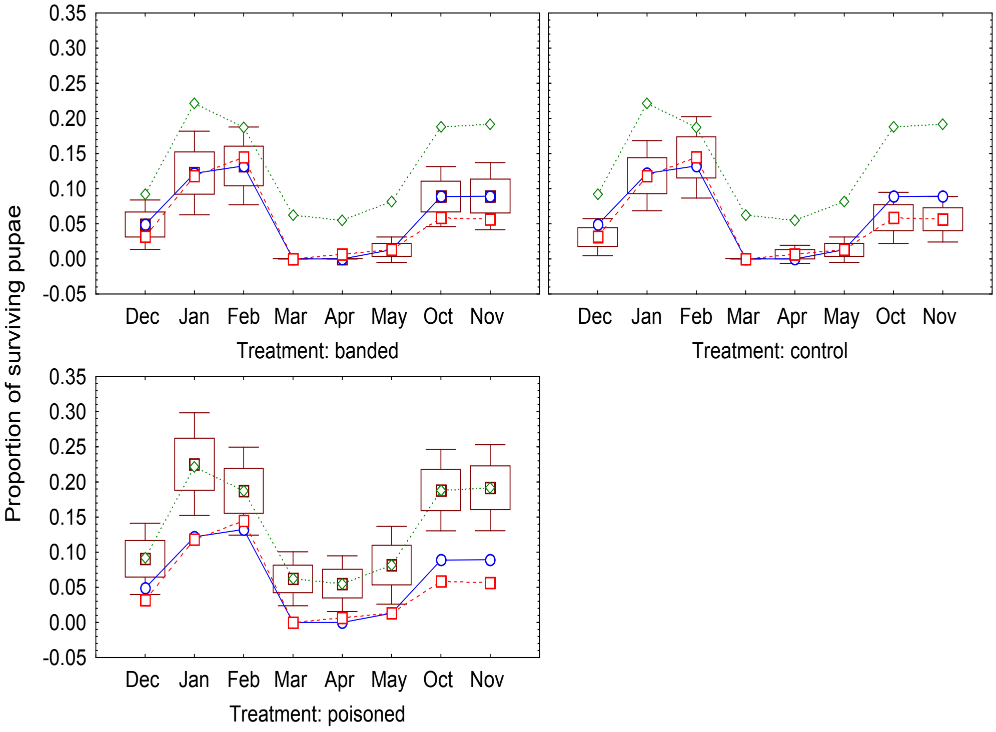

Figure 3.4 Effects of the time of year and treatment and their interaction on the proportion of pupae that survived during all of the trials conducted on Mosslands Farm from December 2000 to May 2001 and October 2001 to November 2001 (95% CI for the mean; ○ banded, □ control, ◊ poisoned).

4

Summary

Citrus crop management focuses on an ecological approach to pest control while maintaining maximum productivity. Emphasis is placed on classical, conservation and augmentation biological control with the use of selective pesticides, which cause minimal or no disruption to natural control agents and the environment, only when necessary. In light of this, any naturally occurring control agents should be conserved and managed in order to maximize their benefits to the crop.

Predators are important biological control agents in agroecosystems and are important in IPM programmes. There is abundant evidence that predacious ants inflict heavy predation on agricultural pests, and can be managed in order to maximize their efficiency in suppressing pest populations. The results reported here show that *P. megacephala* is extremely abundant in citrus orchards and that this species has the potential to substantially reduce the survival rate of soil-pupating citrus pests. Thus, citrus crop management practices, which focus on maximum utilization of natural enemies, should be organised to make use of their benefits.

It cannot be ignored that *P. megacephala* can be a serious economic pest in citrus orchards therefore this species should be managed in such a way that its harmful effects are reduced and its beneficial effects are increased. In terms of crop management and the elimination of economic problems caused by pest ants, ant bands are an ecologically appropriate and effective method of ant control. Beneficial species are left on the ground to prey on soil-pupating citrus pests, and the ant bands do not affect the population levels and thus the efficacy of *P. megacephala* in having a substantial impact on pest populations.

An important point however, is that because honeydew-seeking ants adversely affect the efficacy of biological control agents, emphasis has been placed on controlling pest ants in orchards under biological control. Yet, it seems that ant control is not necessary in biological control orchards as there are insufficient numbers of honeydew-producers to attract the ants in large numbers into the trees. If weeds and grasses are not removed from the aisles between the rows of trees, there is apparently a plentiful supply of food to support high population levels of *P. megacephala*. Therefore, in orchards with an IPM approach, ant control of any kind may not be necessary. If localized outbreaks of homopterous pests do occur, ant bands can then be used.

It cannot be said whether *A. custodiens* is as effective as *P. megacephala* in preying on soil-pupating pests, however, because this species is so sensitive to the availability of honeydew resources, their populations will remain at a low level if trees are banded. Therefore in orchards under biological control or where ant bands are used for ant control, they may not be present in high enough numbers to substantially reduce pest populations.

If the predation and community results are compared, there was a general trend for survival of the pupae to increase with an increase in the age of the trees and for ant species diversity to decrease with an increase in the age of the trees. It seems that predation is more efficient where diversity of the ant fauna is higher. In citrus orchards, habitat modification to promote higher species diversity would be a difficult way of manipulating the ant fauna as the habitat modifies with the changes in the structure of the trees as they mature. A greater diversity of plants within the orchards would lead to higher ant species diversity. Having a variety of grasses and herbs growing between the rows of trees would increase niche and resource availability within the orchards, which would lead to increased ant faunal diversity. This would also aid in maintaining high population levels of *P. megacephala. Pheidole megacephala* is abundant where there are resources on the orchard floor, even in the absence of honeydew-producers in the trees. Although predation on the pupae was more efficient where ant species diversity was higher, the communities in the mature orchards were also beneficial. Climax communities are more stable and once established can be expected to remain intact and thus maintain their influence in that particular area.

Predacious ants and the predator complex as a whole are important natural control agents in citrus orchards therefore conservation of these species will be beneficial. Their maintenance should be considered when chemical control is applied in orchards. By conserving these species, a greater permanence of pest suppression should be obtained with a lower demand for pesticide use. The development of predatory communities in these crop systems would serve well as an aspect in IPM programmes.

These results are not only useful to citrus growers, but are relevant to other tree crops where predacious ants are part of the agroecosystem fauna.

5

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Appendix 1:

Plot and treatment	N (total no. of individuals)	S (total no. of species)	Reciprocal of Simpson's index (1/D)	Evenness (1-D) / max (1-D)	Shannon-Wiener index H′	Evenness H′ / max H′
30a banded	1628	5	1.02	0.0234	0.107	0.0268
30a control	1611	8	1.03	0.0276	0.135	0.0338
30a poisoned	236	4	1.38	0.294	0.79	0.198
30b banded	2233	10	1.04	0.0369	0.177	0.0443
30b control	1583	8	1.04	0.0452	0.195	0.0488
30b poisoned	107	4	1.65	0.416	0.968	0.242
15a banded	625	6	1.64	0.417	1.15	0.288
15a control	544	11	2.37	0.615	1.71	0.426
15a poisoned	117	7	2.78	0.678	1.77	0.443
15b banded	314	8	1.69	0.436	1.19	0.297
15b control	392	9	2.4	0.622	1.72	0.43
15b poisoned	69	8	6.41	0.888	2.72	0.679
4a banded	2556	9	1.13	0.122	0.461	0.115
4a control	3172	7	1.22	0.192	0.654	0.163
4a poisoned	155	7	2.39	0.616	1.7	0.426
4b banded	984	8	1.85	0.489	1.41	0.352
4b control	851	8	1.75	0.458	1.41	0.354
4b poisoned	457	6	2.36	0.613	1.61	0.402
2a banded	1106	10	2.02	0.539	1.52	0.38
2a control	927	10	2.4	0.622	1.83	0.458
2a poisoned	104	6	4.46	0.82	2.29	0.573
2b banded	1003	10	1.39	0.301	0.985	0.246
2b control	700	13	2.83	0.689	2.19	0.547
2b poisoned	74	6	3.16	0.719	2.02	0.504