Towards the development of sustainable control options for the African root and tuber scale on cassava in Central Africa

Understanding the biology and ecology of the tending ant *Anoplolepis tenella* (Hymenoptera: Formicidae)

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TABLE OF CONTENTS

SUMMARY

Anoplolepis tenella Santschi is an afrotropical ant widely distributed in the forest zones of Central Africa. It is the most frequent species associated with the African root and tuber scale (ARTS) *Stictococcus vayssierei* (Hemiptera: Stictococcidae), an afrotropical insect that infests a wide range of root and tuber plants, particularly cassava. Present evidence supports the hypothesis that the scale needs the ant to remove its honeydew secretions, as the scale would otherwise drown in its own secretions. Therefore developing effective management options to reduce ARTS infestations, requires adequate understanding of the biology and ecology of *A. tenella* and its impact on ARTS life cycle and ecology. Therefore, we carried out study on the distribution and abundance of *A. tenella* and thereby co-occurring ant species in mixed-crop fields, fallow and forest which are the dominant vegetation type in southern Cameroon. We also assessed some of the factors that could explain the observed distribution. Results indicated highest species richness in the forest. *Anoplolepis tenella* abundance, density and activity was affected by vegetation type, season and a set of abiotic parameters among which are air temperature and relative humidity. Its abundance was higher in mixed-crop fields, while it was and either absent or rare in the lowland where coincidently *S. vayssierei* was also absent. These results indicate that human activities reduce ant diversity and offer new nesting niches or food sources to ants which could explain the proliferation of species like *A. tenella*. Among other factors affecting the ant's distribution are plants producing nectar and extrafloral nectaries and honeydew producers among which *S. vayssierei*. The distribution of these plants and honeydew-producing insects significantly differed between vegetation types, hence the difference in ant composition. Network analysis of the ant-hemipteran matrix showed high specialization index at individual level for *A. tenella* and *S. vayssierei*. We couldn't demonstrate the dispersal of the scale by air currents or through phoresis on *A. tenella* founding queens. However, through a dispersal experiment in a screenhouse, we demonstrated the active role of *A. tenella* workers in the transport and dissemination of scale crawlers within and between cassava plants. In an effort to control ant colonies under laboratories condition, Boric acid-sucrose solution showed a significant reduction of *A. tenella* population within six weeks. These results demonstrate that control of *S. vayssierei* in crop fields is contingent on reductions in the densities of its associated ant *A. tenella.*

Keys words: Abiotic factors, *Anoplolepis tenella,* ant diversity*,* Boric Acid, control, dispersal, extrafloral nectaries, fallow, forest, honeydew, mixed-crop field, pest, specialization index, *Stictococcus vayssierei*.

RÉSUMÉ

Anoplolepis tenella Santschi est une fourmi largement distribuée dans les zones forestières d'Afrique Centrale. Elle est l'espèce la plus fréquemment associée à la cochenille Africaine des racines et tubercules (CART) *Stictococcus vayssierei* (Hemiptera: Stictococcidae), un ravageur des plantes cultivées principalement le manioc. Les observations au laboratoire et en champ appuient l'hypothèse selon laquelle la présence de la fourmi serait nécessaire pour la survie de la cochenille. Par conséquent, l'élaboration des méthodes de lutte efficace contre la cochenille nécessite une compréhension adéquate de la biologie et l'écologie de *A. tenella* et son impact sur le développement de la cochenille et son écologie. Ainsi, nous avons réalisé l'étude de la distribution et l'abondance de *A. tenella* et des autres espèces de fourmis dans les trois principaux types de végétation qui prédominent dans la zone de forêt humide du Cameroun notamment les champs de polycultures, la jachère et la forêt, Nous avons également évalué certains facteurs qui pourraient expliquer la distribution observée. Les résultats indiquent une richesse spécifique plus élevée dans la forêt. L'abondance, la densité et l'activité de *A. tenella* est affectée par le type de végétation, la saison et une série de paramètres abiotiques parmi lesquels la température de l'air et l'humidité relative. L'abondance est plus élevée dans les parcelles de polycultures et la jachère, faible ou nulle dans les zones de basse altitude, ce qui coïncide également avec l'absence de la cochenille sur les plantes. D'autres facteurs peuvent affecter la distribution des fourmis notamment les plantes productrices de nectaires floraux et extrafloraux, ainsi que le miellat des hémiptères parmi lesquels *S. vayssierei*. La distribution de ces plantes et des hémiptères diffère significativement entre les trois types de végétation, d'où la différence observée dans la composition de fourmis. Les résultats montrent également un indice de spécialisation très élevée pour *A. tenella* et *S. vayssierei.* Nous n'avons pas pu démontrer la dissémination de la cochenille par les courants d'air ou par phorésie sur reines fondatrices de *A. tenella*. Cependant nous avons démontré le rôle actif des ouvrières de *A. tenella* dans la dispersion des larves de cochenille sur les plantes. Nous avons également démontré au laboratoire qu'une solution d'acide borique et de sucre entraîne une réduction significative de la population de *A. tenella* en six semaines. Tous ces résultats démontrent que la lutte contre *S. vayssierei* est subordonnée à la réduction de la densité de *A. tenella* dans les champs.

Mots clés: *Anoplolepis tenella,* Acide Borique, champ de polycultures, diversité, dispersion, facteurs biotiques, forêt, indice de spécialisation, jachères, miellat, nectaires extrafloraux, ravageur, *Stictococcus vayssierei*.

General Introduction

1. Mutualism involving ants

The interactions between living organisms are diverse. For example, in the interaction between a predator and its prey, the predator increases its fitness by consuming the prey. However, exploitation of a resource by a consumer does not always lead to a reduction in the fitness of the resource provider as in the predator-prey system. Considering the network of possible interactions between species, consumption of a resource may also lead to mutual benefits for species interacting. Interaction between two species that confers benefits to both partners is termed "mutualism" (Boucher et al., 1982; Begon et al., 2006). Species, however, differ in their investment in an established mutualism. In facultative mutualism, both partners can survive alone and do not completely require interspecific association. Obligate mutualisms in contrast always find the two partner species in association (Oliver et al., 2008).

1.1. Mutualism between ant and plants

Mutualism between ants and plants involve species in over 100 genera of angiosperms and 40 genera of ants (Davidson and McKey, 1993), and they are of key importance in structuring tropical ant communities (Heil and McKey, 2003). A number of plant characteristics have evolved in response to pressure exerted by herbivores. These adaptations include both structural, physiological and life-history traits (Marquis, 1992). Myrmecophytes, or ant-plants, offer nesting sites to ants and also furnish food in the form of extrafloral nectaries (EFN) or food bodies. EFN represents the most predictable food sources on plant foliage and many ant species are attracted to these glands (Carroll and Janzen, 1973; Bluethgen et al., 2000b; Bluethgen and Fiedler, 2002; Bluethgen et al., 2004). Ants that are attracted to nesting sites offered by plants (domatia) shows a more specific association with the host plants compared to those visiting for nectar. Some of these ant species actively defend the host plant against a broad range of defoliators and pathogens and help in pollination (Heil et al., 1999; Heil et al., 2001; Heil and McKey, 2003; Kocheril and Krishnamurthy, 2009; Rosumek et al., 2009). However, benefits are not always reciprocal, as in numerous instances there are no clear benefits to the plant from ant attendance (Davidson and McKey, 1993; Offenberg, 2000; Mckey et al., 2005; Oliveira and Del-Claro, 2005).

1.2. Mutualism between ants and Hemiptera

Some hemipteran insects of Sternorrhyncha sub-order that includes scale insects, aphids and whiteflies feed from plant phloem. The volume of sap ingested by the insect is very high and the surplus of water, sugar and other elements are excreted in the form of a sugar-rich liquid known as honeydew. Many ant species are attracted to honeydew which supplies their carbohydrate and sometimes amino acid requirements. Therefore, ants benefit from hemipteran insects in term of energy derived from the honeydew, which would result in an increase in the growth rate of the colony (Degen et al., 1986; Buckley, 1987; Hölldobler and Wilson, 1990; Cushman and Addicott, 1991; Delabie, 2001). The abundance of honeydew and other resources derived from plant sap may explain large population densities of dominant arboreal species with their constant high energetic demands (Bluethgen et al., 2000a; Bluethgen and Fiedler, 2002). The benefit derived by hemipterans from ant attendance is classified under four main categories: (1) protection from natural enemies though predatory behaviour, (2) building of shelters around hemiptera aggregation, (3) removal of contaminated honeydew, and (4) dispersal through the transport of juvenile stages and adults to new feeding sites (Way, 1963). For example, ants improve survival rate and reproductive performances of aphid colonies (Buckley, 1987; Flatt and Weisser, 2000); *Acropyga* females are known to carry root mealybugs of the subfamily Rhizoecinae in their mandibles during the nuptial flight for subsequent colony foundation, a behaviour that already existed in Miocene times (Johnson et al., 2001); workers of the weaver ant *Oecophylla longinoda* actively transport their associated coccid *Saissetia zanzibarensis* to new feeding sites on the same or to the nearest host plant (Way, 1954).

Most myrmecophilous honeydew-producing hemipteran, especially aphids and scales, appear to have morphological and behavioral adaptations for obligate association with ants. These adaptations include the inhibition of honeydew ejection, increase of the amount of feeding, short (or absence of) legs in adults, wing loss or delay in their production, and the modification of the life cycle (Gullan and Kosztarab, 1997; Stadler and Dixon, 2005).

1.3. Impact of mutualism on the host plant

Plants cannot directly control resources allocated to the sucking insects and therefore there is potential for a conflict involving mutualism with hemipteran insects. In agricultural systems, mutualistic interactions between ants and hemipteran insects often result in negative

effects on crop plants. In many instances, ants that protect the hemipteran insect pests from their natural enemies cause their proliferation, with associated increase in crop damage with consequent losses in yield and quality. The host plant can be directly affected through the penetration and damage of plant tissues by the insect mouthparts and sucking of plant nutritional resources, or indirectly through contamination of plant surface by uncollected honeydew and sooty moulds, or transmission of arthropod-borne infectious organisms (Cushman and Addicott, 1991; Vranjic, 1997; Delabie, 2001). Therefore, ants associated with hemipteran insects play an important role in the regulation of hemipteran density. When the hemipteran insect density is above a level considered as tolerable for the plant, the presence of the tending ant negatively affects the host plant by stimulating feeding rate and deterring natural enemies of the insect and thus potentially increasing the detrimental effects on plant growth (Buckley, 1987; Bach, 1991).

2. Rationale of the study

The African root and tuber scale (ARTS) *Stictococcus vayssierei* Richard (Hemiptera, Stictococcidae) is an emerging major pest of cassava in Central Africa (Hanna et al., 2004). ARTS is a subterranean insect indigenous to the humid forest zone of Central Africa, home to some of the poorest human populations on the continent, where this insect has increasingly become a major pest of cassava since the mid-1970s. This pest, previously confined to several indigenous plants with tuberous roots has moved onto cultivated crops such as cassava, yams, cocoyam, and groundnut, with the greatest abundance occurring on cassava (Tindo et al., 2009). The pest has been reported from Cameroon, Gabon, Central African Republic, Democratic Republic of Congo (DRC), Equatorial Guinea, Republic of Congo, and extreme western Uganda (Lutete et al., 1997; Ambe et al., 1999; Bani et al., 2003; Ngeve, 2003; Hanna, unpublished data). Yield loss trials from the Bas-Fleuve district of DRC and from Central Cameroon showed that high scale densities could lead to losses of over 60% of cassava root yield and possibly an increase in losses due to cassava root rots (Hanna et al., 2004; Tata-Hangy et al., 2006). A Farmer survey in IITA's Forest Margins Benchmark in Cameroon indicated that ARTS ranked very high as a major pest concern, and is thought to be contributing to approximately 30% of cassava losses (J. Gockowski, Economist, IITA-HFS, unpublished data).

Previous and on-going research initiated in the last few years by IITA in collaboration with national programs from Cameroon and DRC has shed some light on some of the factors that

may have led to the increase in abundance and severity of the scale. Present evidence indicates that scale abundance is affected under certain circumstances by land use patterns prevalent in the forest zone of Central Africa. Scale densities are higher in cassava fields planted after short fallow periods than in fields planted after a long fallow period or after secondary forest. Several indigenous host plants and particularly volunteer cassava are more common in short fallow vegetation compared with long fallow and forest vegetation. Such plants are thought to serve as reservoir for ARTS infesting cassava fields planted after short fallow (Tindo et al., 2009). Moreover, scale abundance in cassava fields is positively related to the degree of disturbed forest cover, and to the frequency of occurrence of a closely associated ant, *Anoplolepis tenella* Santschi (Hymenoptera, Formicidae) which is apparently vital for scale survival and dispersal (Hanna et al., 2004).

Anoplolepis tenella is a ground-dwelling ant species with widespread distribution in Central Africa (Dejean and Matile-Ferrero, 1996). Information on the biology of this ant is meager. Workers of *A. tenella* exploit scale insects and mealybugs on the roots of various plants, and feed on various prey (as protein source), dead or alive, and especially termites (Dejean and Matile-Ferrero, 1996; Fotso Kuate et al., 2008). *Anoplolepis tenella* builds its nest preferably immediately adjacent to crop plants, mainly cassava and other plants infested with ARTS (Fotso Kuate et al., 2006).

The rise in the pest status of ARTS presents an intriguing case on how a native insect **-** which was not considered a pest when it was first described about forty years ago (Richards, 1971) **-** has evolved into a major problem on an exotic crop plant. A major effort is presently underway to identify and characterize biotic, agronomic, and environmental factors that affect scale abundance, and to develop sustainable practices for scale management on cassava and other affected food crops. One of the key questions that must be addressed is the nature of the interactions between *A. tenella* and the scale, and the conditions that promote the abundance of *A. tenella*, which is presently considered the key factor contributing to the proliferation of the scale in Central Africa. As the scale apparently depends on *A. tenella* for its survival, developing options to disrupt ant-scale associations will likely render ARTS a pest of relatively low economic importance for cassava producers who are among the poorest of the poor in Central Africa.

The overall goal of this thesis was to understand the ecology of *A. tenella* and its interactions with ARTS and co-occurring ant species in Central Africa. The thesis is organized into five chapters which correspond to the specific objectives. The first chapter determines the distribution and abundance of *A. tenella* and co-occurring ant species in southern Cameroon; the second chapter assesses biotic and abiotic factors affecting the ant's distribution and abundance; the third chapter assesses the interaction between ants, honeydew-producers and host plants; the fourth chapter determines the role of *A. tenella* in scale dispersal; and the fifth chapter initiates control measure against *A. tenella* colonies.

3. Physical context of the studies

Four locations were selected in the humid forest zone of southern Cameroon based on previous trials and surveys conducted within the framework of the cassava IPM project of the International Institute of Tropical Agriculture (IITA). These four locations were all in the Center region. They included locations (1) Awae II (03° 35'37''N; 011° 36'40''E) which is administratively called Ndangueng in the Mefou-et-Afamba Division; (2) Matomb (03° 48'11''N; 011° 03' 27'' E), (3) Boga (03° 53' 15'' N; 010° 46' 25'' E); and (4) Sombo (03° 53' 36''N; 010° 42' 26'' E). Both Boga and Sombo are in the Nyong-et-Kéllé Division (Fig 1). Awae II and Matomb are upland areas (615 m a.s.l. < elevation < 680 m a.s.l.), while Boga and Sombo are lowland areas (201 m a.s.l. < elevation < 245 m a.s.l.).

3.1 Climate and soil

Climate in the southern Cameroon is equatorial and is classified as humid tropical, characterized by two wet seasons and a short and a long dry season. Rainfall is distributed in a bimodal pattern with greatest accumulation in September-October and April-May. Average rainfall per year is about 2000 mm. Monthly mean rainfall is 200 and 400 mm for April-May and September-October, respectively. October is the wettest month of the year. The two driest periods of the year are December-February and July-August, respectively, with less than 80 mm of rainfall per year. The bimodal rainfall pattern determines two crop growing seasons: the first starts in March and ends in June, while the second starts in August and ends in November. Between the two seasons, from December to March, arable swamps and valley bottoms are cultivated which allows production of off-season food crop. Such a climate has a mean

temperature above 18°C during the coolest month, an annual temperature around 25°C with very little variation during the year, and finally a well delineated dry season (Neba, 1999).

In general, soils in the Congo Basin are predominantly Ferralsols (62%), Nitosols (12%), Ferralic Arenosols (11%), Greysols (5%), Acrisols (2%) and Luvisols (2%) (FAO 2006). Soil in southern Cameroon fall into the FAO grouping of Orthic Ferralsols with the exception of some alluvial soil along the Sanaga River (Yemefack et al., 2006)
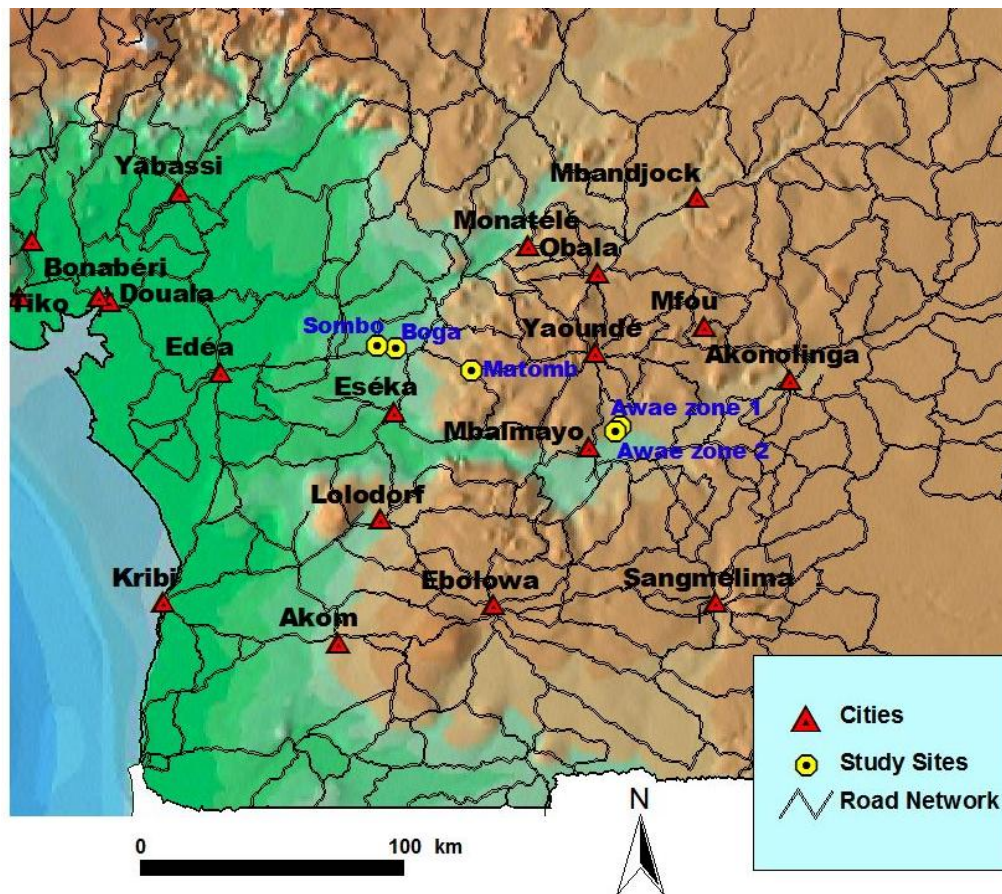
Fig. 1: Map of southern Cameroon with the study sites

3.2 Vegetation type and farming practice

The forest of West and Central Africa is degrading rapidly due to timber exploitation and slash and burn agriculture (ASB, 2003). In the Forest Marging Benchmark Area (FMBA) of southern Cameroon, primary forests cover 3.7% of the area around Yaoundé and 5.3% around Mbalmayo; 39.8% of the FMBA is estimated to be under agricultural use (farmlands, fallows and cocoa plantations); cocoa plantation 8% of the FMBA and over 100,000 ha of fallow is slashed

each year to create farm lands which represent 16.2% of the FMBA (Thenkabail, 1999; Gockowski et al., 2004).

Shifting cultivation has long been considered as the most adapted farming system for the humid forest zone, especially in areas of low population density (Bandy et al., 1993). There is a nutrient flux during slash-burning: ash from burned biomass is incorporated into the soil resulting in an increase in soil fertility. This traditional cultivation pattern, which remains widely practiced in much of the forest zone of central Africa, generally leads to a composite vegetation system which includes slash-and-burn dominant farmlands (also referred to as mixed-crop fields or cassava field), *Chromolaena odorata* (L.) King & H.E. Robins. dominant short-fallows, *Imperata cylindric*a (L.) P. Beauv. dominant weeds, long-fallows or regenerated forests, *raphia* palm-dominant lowlands, permanently flooded swamp forests, and primary and secondary forests. Cash crop plantations are also present covering a significant proportion of the area (Thenkabail, 1999).

Mixed-crop fields are typically established after the slashing and burning of fallow or secondary forest. The dominant crops are cassava (*Manihot esculenta* Crantz) and groundnuts (*Arachis hypogeae*). Others important crops in this system include maize (*Zea may*s L.), plantain (*Musa acuminate* Colla), cocoyam (X*anthosoma mafafa* Schott.), taro (*Colocassia esculenta* [L] Schott.), and a wide range of vegetables (Gockowski and Ndoumbe, 1999; Kanmegne, 2004). Usually, groundnuts and maize are harvested three months later whereas cassava and plantain remain in the field. At maturity, generally six months to one year after planting, cassava is harvested for home consumption, processing or direct selling. Farmers grow crops for a few years, until soil fertility, weed infestation and diseases reduce crop yields below acceptable levels. The plot is then left to a period of restorative fallow during which the soil can recover its fertility if left undisturbed for a number of years.

Fallow vegetation is initially dominated by *Chromolaena odorata* associated with *Sida rhombifolia* L., *Stachytarpheta cayennensis* (Rich.) J. Vahl., *Triumfetta cordifolia* A. Rich. and *Ageratum conyzoide*s L., *Trema orientalis* (L.) Blume, *Cogniauxia podolaena* Baill. and *Mikania cordata* (Burm.f.) B.L. Robinson and other shrubs (Ngobo et al., 2004). Fallows help to re-establish the equilibrium that prevailed initially in the soil before the clearing of the forest. The duration of the restorative period may be extended up to 20 years depending on the land pressure (Mutsaers et al., 1981). In the short fallow systems, there are always some residual food crops

(cassava, plantain, and cocoyam) that remain in the field and provide a certain level of food security for the farming families.

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12

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Chapter 1: Ant diversity in the humid forest zone of Cameroon: Distribution of the pest ant *Anoplolepis tenella* Santschi (Hymenoptera, Formicidae)

Running title: Ant diversity in southern Cameroon

Suggested Journal: Insect Diversity and Conservation

Key Words: Vegetation type, sampling efficiency, β-diversity, *Anoplolepis tenella*, *Stictococcus vayssierei*.

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Summary

1. We conducted intensive ant sampling to determine the patterns of ant diversity and distribution in three predominant vegetation types (forest, fallow and mixed-crop field) in the humid forest zone of southern Cameroon. Three sampling methods were used: baiting, pitfall and quadrat.

2. A total of 237 ant morphospecies in 10 subfamilies and 44 genera were recorded. Almost all the species captured with the baits were also recorded with pitfall and quadrat (Redundancy index R >0.86).

3. Forest had the highest Fisher'α diversity compared to fallow and mixed-crop field.

4. *Anoplolepis tenella* was the second most abundant species after *Myrmicaria opaciventris* and its densities was higher in the mixed-crop fields.

5. Negative association with *A. tenella* was observed with *M. opaciventris* and *Pachycondyla tarsata* in the mixed-crop field and a positive association was observed with *Technomyrmex parandrei* in the fallow.

6. These results indicate that human activities can reduce ant diversity and offer new nesting niches or food sources which could explain the proliferation of species like *A. tenella* in southern Cameroon, and likely the remainder of the Congo Basin.

Introduction

Ants (Hymenoptera: Formicidae) are diverse, abundant and are important components of terrestrial ecosystems (Hölldobler & Wilson, 1990). They constitute a dominant group because of their biomass and diversity and they play important roles in the structure and functioning of ecosystems. Ants act as important herbivores, predators, scavengers, plants pollinators, seeds dispersal agents, and have established mutualistic association with many plants, hemipteran insects (Schultz & McGlynn, 2000) and some groups of butterflies notably in the family Lycaenidae (Hölldobler & Wilson, 1990).

Most work on tropical ant ecology has shown that ants also serve critical functions in agro-ecosystems, especially by influencing the development of pest insects and weed communities (Risch, 1981). In addition to their ecological importance, ants are easily sampled and are responsive to environmental changes (Oliver & Beattie, 1996). For these reasons, ants

have been frequently used to evaluate biotic responses to ecosystem changes (Vasconcelos, 1999).

Considerable attention has been given to the response of ant assemblage to ecosystem disturbance to understand patterns of biodiversity and to assess the potential for using ants as bioindicators (Agosti *et al.*, 2000; Kaspari & Majer, 2000). Many studies concluded that species richness generally declines with increasing disturbance (Vasconcelos, 1999; Watt *et al.*, 2002). The decline of ant species following land disturbance can be related to vegetation composition since it is a major regulator of microclimatic conditions which affect ant activity. However, ant species richness is not always affected by the conversion of the forest to agroforest (Bos *et al.*, 2007).

Vegetation composition can also affect the availability of food resources (presence of plant offering extrafloral nectaries) and nesting sites for ants as well as competitive ability of species (Vasconcelos *et al.*, 2008). In particular, changes in abundance of dominant species mediated by changes in vegetation composition can have major impacts on ant assemblage (Perfecto & Vandermeer, 2006). Dominant species can regulate the structure of ant assemblage by interfering in the foraging activity of other ant species (Savolainen & Vepsäläinen, 1998).

Very few studies on ant diversity have been conducted in Cameroon. Published studies focused on ant diversity in the forest with little attention to the other dominant vegetation types like fallows and farmlands. These two vegetation types are established after complete forest clearance and we would predict that ant diversity is higher in the forest with indigenous tree and low disturbance than in fallow and mixed-crop field which are subjected to anthropogenic disturbances. In this study we assessed the diversity of ant species and the interaction between abundant species in the forest, fallow and mixed-crop field (farmland) in the humid forest zone of Cameroon. Attention was given to the distribution and abundance of *Anoplolepis tenella* Santschi, a species mostly found in the forest area of Central Africa and frequently associated with the African root and tuber scale, *Stictococcus vayssierei* Richard (Hemiptera; Stictococcidae). The scale infests at least ten cultivated crops with greatest occurrence on cassava, and *A. tenella* is considered as one of the factors contributing its proliferation in cassava fields (Dejean & Matile-Ferrero, 1996; Hanna *et al.* 2004; Fotso Kuate *et al.*, 2006; Tindo *et al.*, 2009).

Material and methods

Study area

Research plots were established in four locations in southern Cameroon in May 2007 - in Awae II (03°35'37"N, 011°36'40"E), Matomb (03°48'11"N, 011°03'27"E), Boga (03°53'15"N, 010°46'25"E) and Sombo (03°53'36"N, 010°42'26"E). In Awae II two areas (Awae zone 1 and Awae zone 2) were selected to intensify sampling in that location which is a pilot village for the International Institute of Tropical Agriculture (IITA).

We established sampling plots in dominant vegetation types which included *Chromolaena odorata* short-fallows; slash-and-burn farmlands also referred to as mixed-crop field and long-fallow or regenerated forests. Mixed-crop fields are typically established after the slashing and burning of fallows or regenerated forest.

General method

At each location, six sampling sites representing the three vegetation types (fallow, forest and mixed-crop fields) were selected, giving a total of 30 sampling sites (5 locations x 3 vegetation types x 2 replicates). At each sampling site, a plot of 400 m^2 was delimited 20 m away from the edge of the field. Vegetation structure within plots was homogeneous. In the plot, two parallel transects (10 m apart) were chosen. We used three sampling techniques to assess ant diversity and distribution: pitfall trapping, quadrat sampling and baiting. Six sampling events were conducted at two-month intervals from May 2007 to April 2008. Sampling at Sombo was done four times because the location was added after two sampling events in other locations.

Pitfall trapping

Glass tubes (150 mm length, 21 mm diameter) inserted into plastic pipes were used as pitfall traps. Ten traps were in two rows (10 m apart) of five each, spaced by 5 m. A total of 100 pitfall traps were set up in each vegetation type. Prior to the beginning of sampling, traps were left for two weeks in the field to reduce digging-effect (Greenslade, 1973). During each sampling time, 20 ml of the detergent PAX at 0.02% was filled into the glass tubes. The traps were left open for three days and were protected from rain and falling leaves by an aluminium cover. On the fourth day, ants from each trap were sorted from debris and stored in a plastic vial with 70% ethanol for identification in the laboratory.

Quadrat sampling

We used a dismountable quadrat of $1m^2$-surface to sample in the same design as with pitfall traps, i.e. 10 plots delimited on two random rows of five each. Two consecutive plots in a row were 5-m apart while rows were 10-m apart and perpendicular to pitfall rows. A total of 100 quadrats were sampled in each vegetation type during each sampling event. Each quadrat was checked for five minutes and ant species were collected using Insect Vacuum (BioQuip 2028B) and mouth aspirator. In the forest and fallows, dead leaves, broken twigs and litter were collected and placed on a white mat before the collection of the ants. Ant species were sorted from debris and stored in plastic vial with 70% ethanol for identification in the laboratory.

Baiting

Canned tuna mixed with honey in equal parts was used as ant bait. One teaspoon was deposited on white paper (15 cm x 10 cm) to make the attracted ants more visible. Ten bait stations were placed in the experimental plot. Two consecutive bait stations were 5-m apart. A total of 50 bait stations were set-up for in each vegetation type during each sampling event. During sampling, each bait station was monitored for five minutes, at 30-min intervals during 2 hours. Three periods of the day were studied: morning (between 9:00 and 12:00), afternoon (15:00 and 18:00) and night (between 20:00 and 23:00) in order to take into account differences in daily rhythm of foraging activity behavior of ant species.

Specimen processing

The description of species-rich taxon such as ants remains a challenge for taxonomist. Many species in tropical regions are still to be described. Collected ants were sorted based on external morphology (morphospecies) using keys from the literature (Bolton, 1994) and the online ant resource database (Taylor, 2010).

Data analysis

The presence or absence of ant species in the samples was arranged in a data matrix. The abundance data was not included in the analysis as ants are social organisms and the presence of many individuals could be simply due to collecting a nest or a column of foragers. The presence/absence approach was preferred as some analyses assume that all individuals in the sampling area have an equal probability of being sampled within a spatially and temporally

defined community, which is not the case for the highly aggregated ants (Longino, 2000). We used total occurrence of a species in all the samples to get an estimate of its relative abundance.

The following estimators of species richness were computed to estimate sampling efficiency: Incidence-based estimator of species richness *Chao2* (Colwell & Coddington, 1994); first-order Jackknife estimator of species richness *Jack1* (Heltshe & Forrester, 1983); bootstrap estimator of species richness (Smith & van Belle, 1984); and Michaelis-Menten-Mean (Colwell *et al.*, 2004). These estimators were computed using EstimateS v.8.0 software (Colwell, 2006).

Overlap and complementarity of the ant assemblage in the different vegetation types were assessed through distinctness and beta-diversity indices (Colwell & Coddington, 1994). Complementarity was assessed considering the proportion of all species in two sites that occurred at only one site and was evaluated using the Marczewski-Steinhaus (M-S) distance index: CMS = (a+b–2j)/(a+b–j) where j = number of species found in both vegetation types, a = number of species recorded in the first vegetation type, and b = number of species recorded in the second vegetation type (Colwell & Coddington, 1994). M-S was chosen because of its simple and statistically valid approach to comparing two biotas (Colwell & Coddington, 1994). Beta-diversity (species turnover between vegetation types) was calculated as β = [(a+b+j)/(a/2+b/2+j)]-1. This metric distinguishes between species turnover and the loss of species along a gradient without adding new species (Harisson *et al.*, 1992; Fisher, 2004).

The redundancy of quantitative methods to capture the same portion of the fauna was evaluated using the redundancy index (R): R = 1–*u*/*a*, where *u* = the number of species found only by the method that collected the fewest number of species, and *a* = the total number of species collected that same method (Fisher & Robertson, 2002; Fisher, 2004). Higher values represent greater redundancy: a value of 1 represents complete redundancy, where all species collected by the method that captured the fewest species are also collected by the other method, and a value of 0 represents no overlap between species captured by each method (Fisher & Robertson, 2002; Fisher, 2004).

Differences in species composition among vegetation types

Rather than comparing the number of species between two communities one species at the time, ecological distance measures consider the abundance of all species simultaneously. Considering that ant assemblages can be similar in diversity, but very different in terms of

species composition, canonical correspondence analysis was used compare differences in species composition among vegetation types (Deblauwe & Dekoninck, 2007b). Analysis was done with SAS software version 9.2 (SAS, 2008).

Interaction among abundant species

We conducted path analysis to quantify direct and indirect effect of the five most abundant species on *Anoplolepis tenella* abundance. In this analysis, the standardized partial correlation coefficients that estimate the relationship between the independent variable and the dependent variable is termed path coefficient (Sokal & Rohlf, 1995). Because the independent factors are often correlated, a causal variable can indirectly affect the response variable as a result of its influence on additional causal variable. In our path analysis, the response variable was *A. tenella* abundance whereas the independent variables were abundances of each of the co-occurring ant species. To capture the impact of variability in species occurrences on their interactions and effect on *A. tenella*, the analysis was conducted by vegetation type. Analysis was done with SAS software version 9.2 (SAS, 2008).

Results

Taxonomic structure of the ant assemblage

A total of 237 species or morphospecies in 10 subfamilies and 45 genera were recorded in the three vegetation types in southern Cameroon. The total occurrence - number of times each species was recorded, regardless of the number of individuals - was 11479. With 126 species in 18 genera, Myrmicinae dominated the other subfamilies in taxonomical richness, followed by Formicinae (50 species in 8 genera) and Ponerinae (34 species in 10 genera). The most species-rich genus was *Tetramorium* (34 species) followed by *Crematogaster* (25 species) and *Camponotus* (25 species). Myrmicinae also had the higher total species occurrence (4823), followed by Formicinae (3513) and Ponerinae (1697). *Myrmicaria opaciventris* was the most common species (1027 occurrences), followed by *Anoplolepis tenella* (952 occurrences), *Technomyrmex parandrei* (533 occurrences)*, Pachycondyla tarsata* (497 occurrences)*, Camponotus maculatus* (392 occurrences)*, Paratrechina weissi* (379 occurrences) and *Tapinoma carininotum* (369 occurrences) (Annex 1).

Overall, observed subfamilies and genera were similar in the three vegetation types. Forest plots had the highest Fisher'α diversity index (average ± SE: 49.26 ± 3.71) followed by fallows (average ± SE: 41.52 ± 4.02) and mixed-crop fields (average ± SE: 26.11 ± 2.81) (Figure 1). Randomized species saturations are displayed in Annex 3 and Annex 4. Others measures of species diversity are displayed Annex 5.
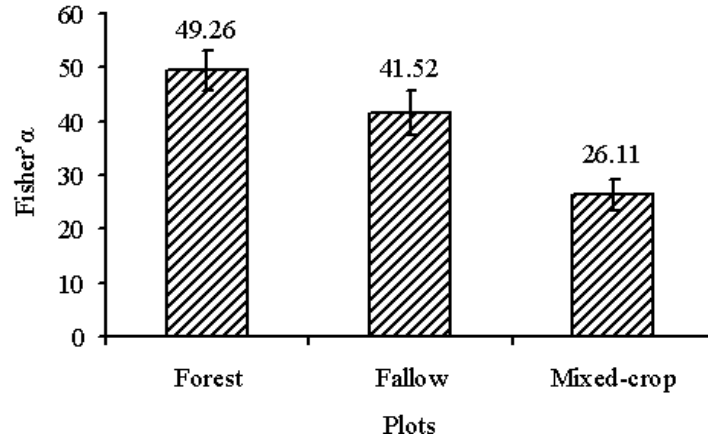
Fig. 1. Fisher'α diversity for ant species in the forest, fallow and mixed-crop field.

Ninety nine species (39.0%) were recorded in all three habitats, 81 (31.9%) occurred in two habitats and 74 (29.1%) in one habitat: 45 species (17.7%) in the forest; 21 species (8.3%) in the fallow and 8 species (3.1%) in the mixed-crop field. Measures of species turnover (β) and distinctness (M-S) between vegetation types were not similar. The forest and mixed-crop field had the greatest species turnover (β = 0.37) and distinctness (M-S = 0.55), while the forest and fallow sites had the lowest (Table 1).

Table 1: Complementarity and species turnover between the three vegetation types based on all sampling methods. The Marczewski-Steinhaus (M-S) complementarity measure is above the diagonal and the Harrison index of beta diversity is below. Higher values represent greater distinctness (M-S) or species turnover (β). The number of species shared by two vegetation types is presented in parentheses.

Vegetation type	Fallow	Forest	Mixed
Fallow (180 spp.)	-	0.370 (155 spp.)	0.435 (118 spp.)
Forest (191 spp.)	0.222	-	**0.549** (105 spp.)
Mixed (127 spp.)	0.276	**0.371**	-

Sampling efficiency in the three type of vegetation

In all comparison we used the total number of ant species recorded within each vegetation type and by each method. None of the three methods captured all ant species in the different vegetation types. Quadrat sampling yielded on average 73.27 ± 6.43 species, followed by pitfall trap (45.67 ± 3.11 species) and bait (25.87 ± 2.62 species). The redundancy index (R) clearly showed an overlap of species captured by each method ($0.86 \leq R \leq 0.98$). Baiting was more redundant with pitfall and quadrat in the three vegetation types ($0.97 \leq R \leq 0.98$), with highest redundancy (0.98) in mixed-crop field. The cumulative number of species using optimal order of methods showed that baiting contribution to the total number of species is insignificant (Table 2). Almost all the species recorded by this method were also recorded by quadrat and pitfall (113 species out of 115).

Table 2. Optimal order of methods to capture the greatest number of species for vegetation type, based on the 3 sampling methods used in this study. The cumulative number of species captured is in parentheses. B = baiting, P = pitfall trap and Q = quadrat.

Vegetation type	Methods
Fallow	Q(161) + P(177) + B(180)
Forest	Q(177) + P(189) + B(191)
Mixed	Q(117) + P(126) + B(127)
All	Q(224) + P(234) + B(237)

Observed species richness in mixed-crop field (65.80 ± 6.85 species) was lower compared to that recorded in fallow (97.6 ± 11.9 species) and forest (104.40 ± 11.84 species) (Table 3). Based on mean estimators, forest presented greater species richness (141.61 ± 6.76) compared to fallow (129.82 ± 7.33) and mixed-crop field (84.04 ± 5.01). The later significantly differed from the two others ($F_{(2,57)} = 22.24$; $P < 0.0001$). We observed the same tendency in all the sampling locations with the exception of Awae zone 2 and Matomb where significant difference was found between each pair of vegetation types.

Table 3. Average number of ant species recorded with the three sampling methods in each vegetation type. Means were calculated from five points representing the number of species recorded in the different vegetations type in the five sampling locations.

Methods	Vegetation types			All vegetation
	Fallow	**Forest**	**Mixed**	
Quadrat	80.2 ± 10.88	87.0 ± 10.54	52.6 ± 6.25	73.27 ± 6.43
Pitfall	48.4 ± 6.55	47.20 ± 6.08	41.4 ± 3.85	45.67 ± 3.11
Baiting	33.0 ± 3.99	25.20 ± 3.94	19.4 ± 4.17	25.84 ± 2.62
All methods	97.6 ± 11.9	104.4 ± 11.8	65.8 ± 6.90	

When we considered the tree vegetation type, species richness in mixed-crop field differed significant between the sampling locations ($F_{(4,15)} = 20.52$; $P < 0.0001$). Species richness in the forest significantly differed between highland (Awae and Matomb) and the lowland (Boga and Sombo) ($F_{(4,15)} = 15.68$; $P < 0.0001$). Species richness in fallow at Sombo was the lowest and differed from other locations ($F_{(4,15)} = 16.43$; $P < 0.0001$). Other significant difference was observed between Awae (zone 1) and Matomb, Boga and Sombo.

Ant assemblage pattern

The correspondence analysis between the species with occurrence greater than 100 (29 species) across the five locations and in the three vegetation type is presented on Figure 2. From the first dimension we can observe that *Camponotus agonies, Monomorium angustinode, Monomorium bicolor, Monomorium vaguum, Pheidole schultzei, Pheidole squalid, Pheidole termitophila, Tetramorium sericeiventre and Tetramorium simillimum* are likely to be associated with mixed-crop field. *Anochetus africanus, Pachycondyla soror, Pachycondyla tarsata, Pheidole dea, Pheidole pulchella, Pheidole speculifera, Polyrhachis militaris, Technomyrmex lujae, Tetramorium guineense, Tetramorium magnificum, Tetramorium sp* are likely to be associated with forest (Figure 2). *Camponotus haereticus, Camponotus brutus, Cataulacus guineensis, Oligomyrmex sp, Pachycondyla ingesta, Pachycondyla ambigua, Polyrhachis aerope* and *Polyrhachis decemdentata* are associated with fallow. *Anoplolepis tenella* coordinates on the graph is best determined by mixed-crop field.
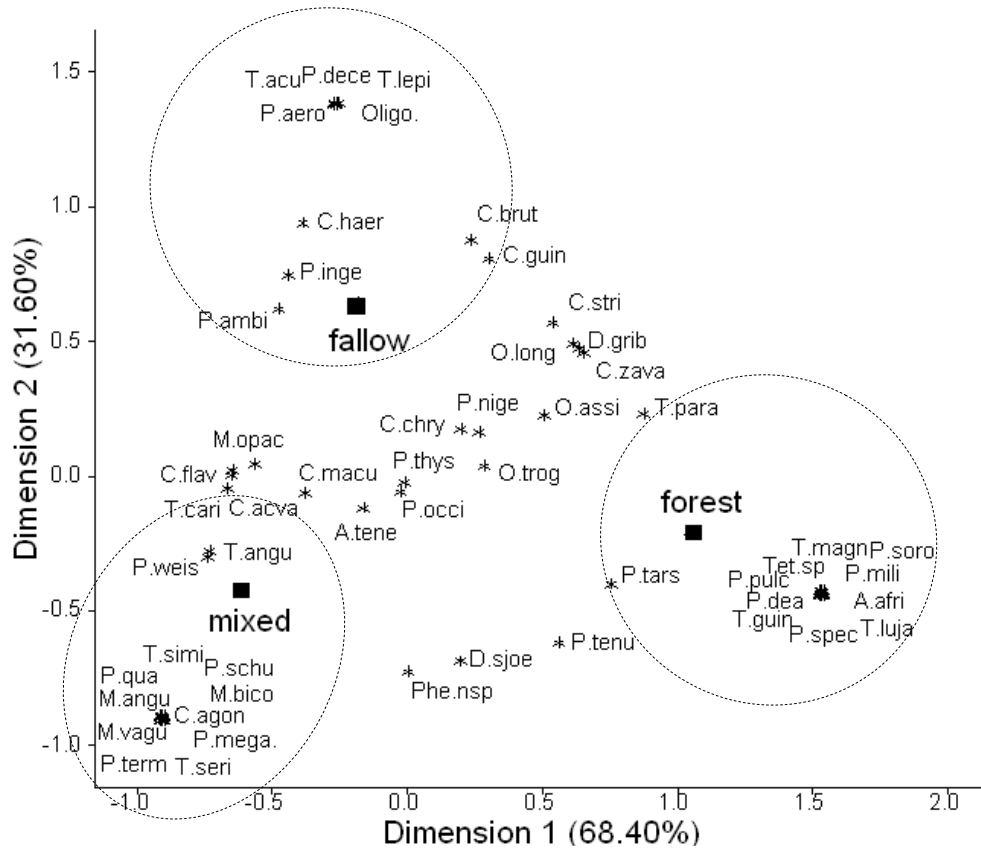
Fig.2. Simple Correspondence Analysis of vegetation type and their ant assemblage. Only the 30 most abundant species in each vegetation type were included in the analysis (Association between species and vegetation type: χ^2 = 6157.5, df= 104, P < 0.0001). For complete name of ant species see Annex 1.

Interaction between some abundant species

In the fallow, direct effect coefficients on *A. tenella* was higher for *T. parandrei* (0.62) followed by *M. opaciventris* (0.25) and *Tapinoma carininotum* (-0.16). Net effect was positive for *T. parandrei* (0.60) and negative for *Pachycondyla tarsata* (-0.29) and *Tapinoma carininotum* (-0.24). The net effect of *Myrmicaria* was nearly insignificant (0.03).

In the forest, direct effect coefficients on *A. tenella* was higher for *Pachycondyla tarsata* (0.37) followed by *T. parandrei* (0.32). Net effect was positive for *T. parandrei* (0.50) and *Pachycondyla tarsata* (0.53) and *T. parandrei* (0.50), and negative for *M. opaciventris* (-0.05).

In the mixed-crop field direct effect coefficient on *A. tenella* was higher for *P. tarsata* (-0.25), followed by *M. opaciventris* (-0.23). The net effect was negative for *P. tarsata* (-0.22) and *M. opaciventris* (-0.12).

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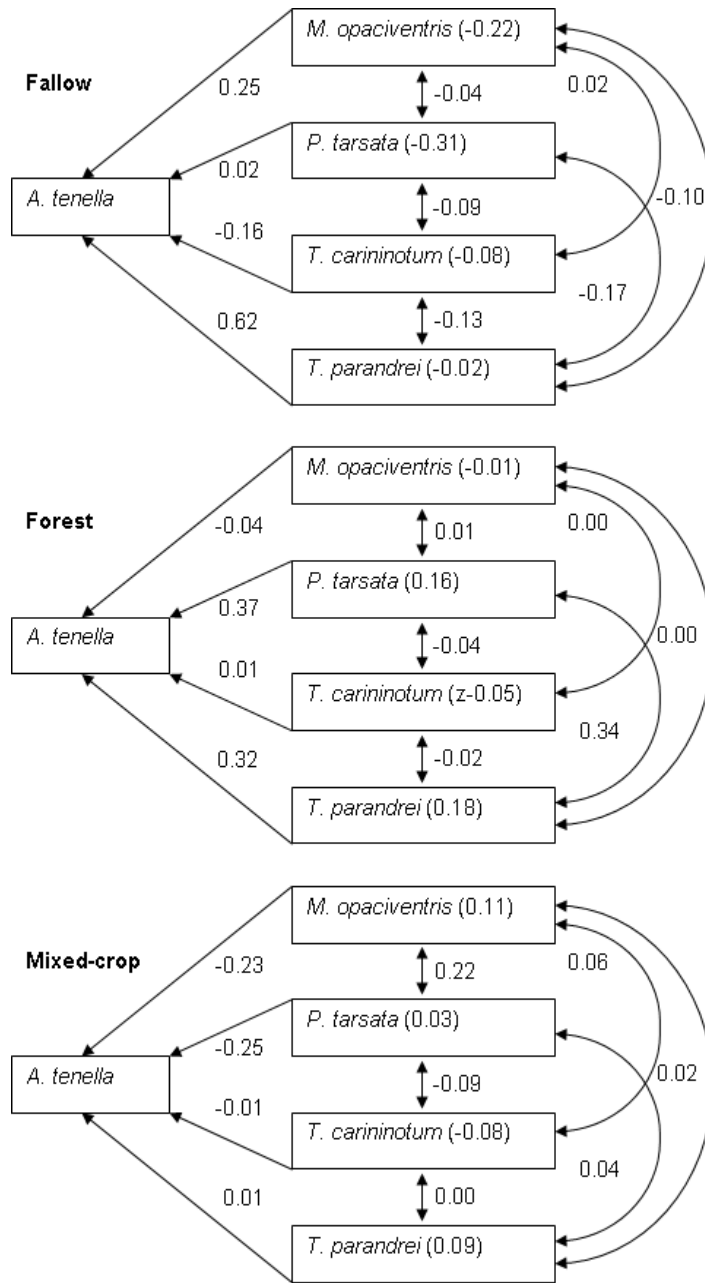
Fig. 3. Path diagram analysis showing the direct and indirect effects of most abundant co-occurring ant species on *Anoplolepis tenella* abundance in the three vegetation types. Single headed arrows indicate direct effect (path coefficients) of each species on *A. tenella* abundance. Path coefficients accompany these arrows. Double headed arrows indicate interaction among co-occurring species and are also accompanied by appropriate simple correlation coefficients. Total indirect effect of each species is shown in brackets in front of the species name. For complete name of ant species see Annex 1.

Discussion

This study outlines the distribution patterns of ground-dwelling ants along a gradient of forest disturbance in southern Cameroon. The results presented here provide evidence that forest loss leads to a reduction in species richness. With 237 morphospecies recorded, our sampling effort yielded more species compared with those recorded in previous studies: 80 species in the forest marging benchmark or Southern Cameroon (Birang, 2004); 145 species in Southeast Cameroon (Deblauwe & Dekoninck, 2007a), 111 species from the litter in the Mbalmayo forest reserve (Watt *et al.*, 2002). It is, however, far below the 310 species recorded in nearest Gabon at Monts Doudou (Fisher, 2004). The later study used a combination of seven sampling techniques to attain such higher species richness. Beside, our study included both undisturbed and disturbed areas while the former were mostly conducted in undisturbed areas. This could have contributed to the sampling of fewer number of ant species.

Mixed-crop field had the lowest Fisher'α diversity index compared to fallow and forest. Because of the incomplete sampling of the ant fauna during this study (sampling efficiency between 68-86%), this measure is considered as a good diversity index (Beck & Schwanghart, 2010). It presents therefore a decrease in species richness from forest to mixed-crop field. Sampling efficiency is known to be influenced by effort, the density of the insects, their activity and size and/or the influence of the sampling technique on the targeted insect (Dewar *et al.*, 1982). Pitfall traps performance was less than quadrat samples especially in the forest. In this vegetation type, we recorded on average 46 ant species (range: 40-50) in 90 traps (range: 80-100) per sampling event. This efficiency was lower compared with other studies: 56 species in 56 traps during 5 days in the Dja reserve with pitfall (Deblauwe & Dekoninck, 2007b), 111 species in 70 samples with Winkler extraction at the Mbalmayo Forest Reserve (Watt *et al.*, 2002). It was however higher than the number of species collected with pitfall traps by Fisher (2004) (14 species in 33 traps during 7 days at 375 m). The variation between traps size between these studies can explain these differences. The internal top diameter of our traps was 21 mm, which was smaller, compared to 285 mm used at Monts Doudou (Fisher, 2004) or 100 mm used in southeast Cameroon (Deblauwe & Dekoninck, 2007a; Deblauwe & Dekoninck, 2007b).

Our results corroborated the fact that human activities affect ant communities (Vasconcelos, 1999; Watt *et al.*, 2002). Habitat modification causes changes in a series of abiotic and environmental factors, especially temperature and humidity, which are among the most

important physical factors affecting ecological processes. These factors also have influence on plant growth rate and survival, seedling establishment, physical soil properties, microbial activity and occurrence of insects (Campbell, 1994). Greater distinctness between mixed-crop field and forest could therefore be attributed to the variation of environmental factors between these vegetation types. However, because we don't know the identity of the missing species and the robustness of the beta diversity analysis, these results could change if the missing species were collected.

Mixed-crop fields had the lowest species richness compared with fallow and forest. Most of the species not found in the mixed-crop fields are known to be arboreal and included species of the genera *Crematogaster*, *Tetraponera, Polyrhachis* and *Cataulacus*. These species leave their nests in the tree to forage on the ground where they were sampled. The absence of their nesting trees in the mixed-crop field could explain their low abundance or absence in this vegetation type, thus supporting the effect of vegetation structure on species distribution. Many studies invoked at least one of several plant attributes (e.g., richness, biomass, and percentage of cover) as a causal mechanism affecting ant diversity (Caldas & Moutinho, 1993). Plants offering extrafloral nectaries (ENFs) or hosting hemipteran are also known to structure ant communities through their bottom-up effect (Bluethgen *et al.*, 2004). The distribution of these EFN-plants is reported to differ significantly between the three vegetation types and the presence of honeydew-producers significantly affect the abundance of trophobiotic species like *A. tenella* (Fotso Kuate et al., in prep).

Unlike for ant diversity, the abundance of some species such as *A. tenella* increases sharply when forests are converted to mixed-crop field. Increase in ant activity was also observed when natural forest was converted to cocoa plantation (Migge-Kleian *et al.*, 2007). This change in ant abundance, along with reduction in fallow age, has caused in turn the proliferation of the hemipteran *Stictococcus vayssierei* on cassava, the dominant host plant in mixed-crop fields (Dejean & Matile-Ferrero, 1996; Fotso Kuate *et al.*, 2006; Tindo *et al.*, 2009). Studies on the congeneric ant *Anoplolepis gracilipes* in indonesian agroforest showed that habitat modification promoted the occurrence of this invasive species probably because other ant species was negatively affected by the management which may offer nesting sites or food sources to generalist ants (Bos *et al.*, 2007)

28

Our results also suggested associations between some abundant ant species. The most noticeable of these is the negative effect of *M. opaciventris* and *P. tarsata* on *A. tenella* in the mixed-crop field and the positive interaction between *A. tenella* and *T. parandrei* in the fallow. Measuring association between species provide insight of the extent to which species are naturally grouped within a community. Several factors can lead to positive or negative association between species. These include similarities in habitats requirements, interspecific association resulting from species interaction, food chain co-action, or similarities in adaptation and response to the environment (Kershaw, 1973). When two species have overlapping habitat requirements or one species modifies the milieu in a way that allows the installation of another species, positive associations are expected. This could be the case between *A. tenella* and *T. parandrei* in the fallow and forest, between *A. tenella* and *P. tarsata* in the forest which have overlapping habitats. However positive association does not always mean that one species is beneficial to the other. It may just result from the sampling units which offered better environmental condition for both species (Pielou, 1974).

Negative associations occur when two species possess different habitat requirements or interact in such a way that is detrimental to one or both species (Pielou, 1974). Interspecific competition between two species can involve either food source or nesting sites (Morrison, 2000). If the overall effect of a competitor does not allow to the complete exclusion of the other species, then the reduction in the fitness of the other species will lead to negative association (Pielou, 1974). *A. tenella* and *M. opaciventris* display similar foraging pattern and may compete for resources in the mixed-crop field, thus justifying the negative association (Kenne & Dejean, 1999; Fotso Kuate *et al.*, 2008). It is less likely that *A. tenella* and *P. tarsata* compete for food sources or nesting sites. *P. tarsata* is a predator and scavenger (López *et al.*, 2000) and it is frequent in the forest (Deblauwe & Dekoninck, 2007a), while *A. tenella* is a generalist ant and frequent in the mixed-crop fields (Fotso Kuate *et al.*, 2006; Fotso Kuate *et al.*, 2008). Therefore the negative association observed between these two species in the mixed-crop could be attributed to difference in habitats requirement.

In conclusion, forest loss leads to a reduction in arthropod species richness (Beck *et al.*, 2002). Moreover, conversion of forests to farmlands can have serious consequences, among others, through proliferation of insect pests (such as *A. tenella* and *S. vayssierei*). Other factors

such as the reduction in environmental regulatory capacity could also be explored during further studies.

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Chapter 2: Seasonal variation in ant species richness, abundance, density and activity in the humid forest zone of southern Cameroon

Running head: Effect of vegetation and season on ants in southern Cameroon

Suggested Journal: Insectes Sociaux

Key words: Season, vegetation type, temperature, humidity, *Anoplolepis tenella*, *Stictococcus vayssierei*

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Abstract

We surveyed three vegetation types in the humid forest zone of southern Cameroon to determine the influence of season, temperature, humidity, and soil characteristics on ant species. Ants were sampled using baits, hand-collecting in quadrats, and pitfall traps. Six sampling events were performed from May 2007 to April 2008. Ant species richness, abundance, density ant composition was affected by vegetation, season, air temperature and relative humidity, and soil characteristics. *Anoplolepis tenella* abundance and density and activity were affected by vegetation type and not by the season. In contrast, its activity was influenced by vegetation, season and the interaction between these two factors, soil and air temperature, air relative humidity and soil characteristics. Its density and activity were higher in mixed-crop fields and can be directly related to the presence of the cassava pest *Stictococcus vayssierei* to which it is associated. Our results suggest that ant assemblages are dynamic and their activity and density are driven by vegetation composition. Observed differences can be postulated to be linked to the disparities of biotic and abiotic factors between these vegetation types.

Introduction

Ant diversity, abundance, and nest distribution are influenced by several environmental factors. Understanding factors that determine the distribution and abundance of plants and animals remains a major field for ecological studies (Symonds et al., 2006). In particular, ecological factors that influence the distribution of ants have attracted considerable attention for two reasons. First, ants represent a substantial fraction of the biomass and are a major force that structures communities (Hölldobler and Wilson, 1990). Second, the density of colonies and ant abundance can be influenced by several factors including longitude, latitude, relative humidity and several soil attributes (Milks et al., 2007).

Two broad categories of factors affect the occurrence of species in an environment: abiotic conditions (Moyle and Light, 1996; Blackburn and Duncan, 2001) and species interaction (Torchin et al., 2003). Physical factors such as solar radiation, temperature, humidity and water availability could play an important role in determining ant diversity (MacKay, 1991; Bestelmeyer, 1997). In arid or semi arid environments, for example, high solar radiation, fluctuation of temperature and low precipitation impose severe conditions that limit the

distribution and abundance of some ant species (Rios-Casanova et al., 2006). Most ant species forage at temperatures between 10 and 45°C. Temperature out of this range may be considered stressful (Hölldobler and Wilson, 1990). Because they are so sensitive to habitat variation and respond quickly to changes in habitat quality, ants are excellent indicators of land management practices and restoration efforts (Andersen and Majer, 2004).

Vegetation structure and soil physical properties are factors that modify environmental conditions and consequently affect ant diversity and distribution (Johnson, 2000; Johnson and Ward, 2002). Several plant attributes (e.g., richness, biomass, and percentage of canopy cover) are also postulated as a causal mechanism affecting ants (Vasconcelos, 1999; Fisher and Robertson, 2002). The density of the vegetation cover affects the quantity of solar radiation reaching the ground, and hence water evaporation and soil temperature. Therefore, dense vegetation such as forest provides better nesting condition and favor activity of species adapted in moist forest - e.g. *Formica lugubris* - compared to site with simple vegetation structures which may be adapted thermophilous species (Arnan et al., 2009). Difference in vegetation composition can also affect the distribution of plants offering foods to ant, which could therefore affect ant species composition (Johnson, 2000). Likewise, soil characteristics can influence the moisture and soil temperature inside ant nests. This study focuses on biotic and abiotic factors that may affect ant species in three dominant vegetation types in the humid forest zone of southern Cameroon. Emphasis was placed the pest ant *Anoplolepis tenella* Santschi which is associated to the proliferation of the African root and tuber scale, a cassava pest in Central Africa.

Material and methods

Study area

Research plots were established in four locations in southern Cameroon in May 2007. They were Awae II (03°35'37''N, 011°36'40''E), Matomb (03°48'11''N, 011°03' 27''E), Boga (03°53'15''N, 010°46'25''E) and Sombo (03°53'36''N, 010°42'26''E). Awae II and Matomb are situated in the upland area (615 - 680 m a.s.l.) while Boga and Sombo are situated in the lowlands (201 - 245 m a.s.l.).

The vegetation in southern Cameroon is composite and includes slash-and-burn dominant farmlands typically established after the slashing and burning of fallows or secondary forest;

Chromolaena odorata dominated short-fallows, *Imperata cylindrica* dominant weeds lands, long-fallows or regenerated forests, raphia palm-dominated lowlands, permanently flooded swamp forests, and primary and secondary forests. Cash crop plantations are also present in covering significant proportion of the area (Thenkabail, 1999). The climate is characterized by the season sequences long dry season-short wet season-short dry season-long dry season-two wet season. Average annual rainfall is about 1600 mm an average temperature is around 23.5°C (Neba, 1999).

General method

In each location, three complementary sampling techniques (pitfall trap, quadrat sampling and baiting) were used to monitor ant diversity and abundance in three vegetation types (fallow, forest and mixed-crop fields). Each vegetation type was replicated twice in each location. Sampling was conducted at two months interval from May 2007 to April 208. The sampling methods are described below.

(1) Pitfall traps: ten traps (160 mm deep, 21 mm top internal diameter) were set up at 20 m from the edge of each vegetation type, arranged in two rows of five traps each. Traps in a row were 5 m apart, while traps between rows were 10 m apart. Prior to the beginning of the sampling, traps were left for two weeks in the field to reduce the digging-effect (Greenslade, 1973). A total of 100 pitfall traps were set in each vegetation type.

(2) Quadrat: we used a plastic pipe (Ø: 18 mm) to make a dismountable quadrat of $1m^2$-surface. Sampling design was the same as with pitfall traps (10 quadrats delimited on two random rows of five each). Two consecutive plots in a row were 5-m apart while rows were 10-m apart and perpendicular to pitfall rows. Each quadrat was checked for three minutes and ant species were collected using Insect Vacuum (see BioQuip 2028B). In the forest and fallows, dead leaves, broken twigs and litter were collected and placed on a white mat before the collection of the ants with mouth aspirator and forceps.

(3) Baiting: bait was a mix of canned tuna and honey in equal parts. One teaspoon was deposited on white paper (15 cm x 10 cm) to make attracted ants more readily visible. Ten bait stations were placed on a random transect in the experimental plot. Two consecutive baits were distant by five meters. Each bait station was monitored for five minutes, at 30 min interval

40

during two hours in the morning, at midday and in the evening to take into account differences in daily rhythm of foraging activity behavior of ant species.

Abiotic parameters

Air temperature and relative humidity (RH)

One Hobo Pro v2 logger (Onset Computer Corporation, MA, USA) was set in each vegetation type for daily recordings of air temperature and relative humidity at one hour intervals. Each hobo was fixed on a metallic plate (15 cm x 10 cm) that was suspended on a vertical support at 150 cm above the ground surface. The metallic plate was shaded with a polyethylene plate (30 cm x 25 cm) to avoid direct contact with sunlight.

Soil temperature

Soil temperature was measured in the different vegetation using a Thermocouple Thermometer Barnant Model 600-1010. It recorded soil temperature over the total length of the sensor. Measurements were done in the morning (8:00-10:00) and afternoon (16:00-18:00). Measurements were made in open as well as shaded areas. Two levels of depth were considered (12.5 cm and 20 cm below the soil surface). The latter corresponds to the average nest depth of *Anoplolepis tenella* which was estimated at 19.7 cm (Fotso Kuate et al., 2006).

Soil Characteristics

Soil samples were collected in a regular pattern on a grid in each vegetation type under investigation. The starting point was located by a random process, but five meters from the edge of the vegetation type. Two consecutives samples were ten meters apart. Six samples were collected per vegetation type. 250 g of soil were collected with a probe from the soil surface to 30cm depth and kept in labeled paper bags. For each sample, we determined the pH, the soil organic carbon, the soil total nitrogen and the organic matter.

Rainfall

Rainfall was recorded daily at each location. A rain gauge was fixed to a pole at 120 cm above ground level and was left completely exposed to the air.

Ant species parameters

Species richness, density and abundance

Species richness was expressed as the observed number of ant morphospecies per vegetation type. We estimated ant species density expressed as the number of species per m^2 in each vegetation type. Thus only data from the quadrat sampling was used to estimate the ant density.

Abundance of each species was expressed as the total number of time the species was collected regardless the number of individual in the sample (total occurrence). This approach was used because the presence of numerous individuals in a trap species may be related to colony movement or recruitment to a food source.

Species activity

For species activity, we used only data from pitfall traps. It was expressed as the sum of individuals of species captured in the pitfall trap. Pitfall traps were chosen because they operates on their own without the acting presence of the sampler (passive method) and they also operate longer in the field compared to quadrat and bait sampling. Activity data was log-transformed for analysis to reduce the variance that may be caused by species that form column during foraging or nest movement.

Analysis of environmental factors and effects on ants species parameter

Principal Component Analysis (PCA) was used to reduce the number of correlated abiotic parameters to four most important axes (software SAS, version 9.2). Association between the environmental parameters and PCA axis was assessed based on eigenvectors (variable loadings), with coefficients ≥ 0.30 or ≤ -0.30 considered as highly associated.

We used spearman rank correlation to evaluate the relationship between ant parameters, and between these parameters and the four significant PCA axes. Analysis was done with the software SAS 9.2. Significance at $p=0.05$ was determined using Least Square means (LS-means). Effect of vegetation, season and the four PCA axes on ant parameters was evaluated simultaneously in the General Linear Model that used vegetation and season as class variable,

42

and the four axes as quantitative variables. Vegetation was crossed with each of the four axes in the model.

Because two vegetation types can have the same species richness but differ in the composition of ant assemblages, we used a distance-based test for homogeneity of multivariate dispersion with the program PERMDISP to test the effect of vegetation and its interaction with season on ant species composition (Anderson, 2004). PERMDISP compares the multivariate dispersions among groups on the basis of any distance or dissimilarity measure. We chose the Chi-square distance index with 9999 permutations.

Results

Environmental parameters

Rainfall

The rainfall pattern during the study period is displayed on Figure 1. From the figure, we delimited the six periods during which the six sampling events occurred. We could distinguish the short wet season (SW07) from May to mid July; the short dry season (SD07) from mid July to mid August; the long wet season (LW07) from mid August to mid November; the long dry season (LD08) from mid November to February and the short wet season (SW08) from March to April. Because the fifth and the sixth sampling were conducted in a different year (January 2008 and April 2008), their corresponding seasons (LD08 and SW08) and were separated from those of the previous year.
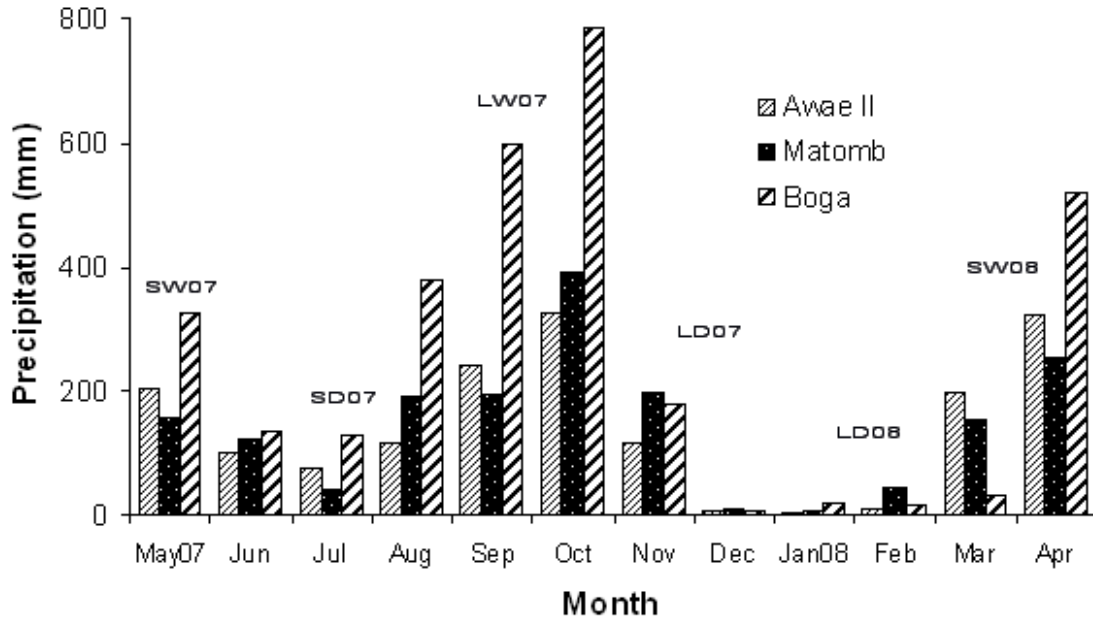
Fig.1 Rainfall pattern during the study period with the six sampling events, corresponding to the six seasons. The short wet season (SW07); the short dry season (SD07); the long wet season on (LW07); the long dry season (LD07); the long dry season (LD08) and the short wet season (SW08).

Air temperature, air relative humidity, soil temperature and soil characteristic

Mean values of these parameters are displayed in Annex 6 and Annex 7. PCA analysis of these parameters showed that the first four axes significantly explained 85.5 % of the variance in the abiotic variables (Table 1). The first axis (Prin1) was positively associated with air and soil temperature and can be considered as the measure of air and soil temperature at different levels, as is evidenced by the same magnitude of the coefficients corresponding to all those variables. The second component (Prin2) has a considerable positive coefficient on soil organic Carbon (0.56), soil total nitrogen (0.50) and organic matter (0.50). The third component (Prin3) has a considerable negative coefficient on soil pH (-0.37), organic matter (-0.38), total nitrogen (-0.33) and positive coefficient on air humidity (0.53) and the ratio C/N (0.64). The fourth component (Prin4) is associated with the soil pH (0.75) and the air relative humidity (0.48).

44

Table 1: Eigen values, percentage (%) of variance explained and eigenvector coefficients of the environmental parameters for the four significant axes of the principal components analysis (PCA). (Associated parameters are in bold)

Parameters	Prin1	Prin2	Prin3	Prin4
Eigenvalue	6.00	3.05	1.09	0.98
Cumulative Percentage	46.16	69.61	78.00	85.55
pH	0.11	0.17	**-0.37**	**0.75**
Organic C	0.07	**0.56**	0.03	-0.08
Total N	-0.01	**0.50**	**-0.33**	-0.15
Organic Matter	0.03	**0.50**	**-0.38**	-0.08
C/N	0.19	0.24	**0.64**	-0.03
Air RH	-0.20	0.11	**0.53**	**0.48**
Air Temperature	**0.34**	0.13	0.14	0.08
Soil temperature, open	**0.36**	-0.07	0.00	0.18
Soil temperature, shade	**0.37**	-0.04	0.06	0.18
Soil temperature, afternoon	**0.32**	-0.09	-0.03	-0.17
Soil temperature, morning	**0.35**	-0.05	0.00	-0.24
Soil temperature, 12.5 cm	**0.39**	-0.05	-0.00	-0.01
Soil temperature, 20 cm	**0.39**	-0.04	0.07	0.00

Species richness (Total number of species)

We recorded 237 ant species in the three vegetation types. Average species richness was affected by vegetation type ($F_{(2,78)} = 9.21$; P = 0.0004). It did not differ between fallow (26.69 ± 1.09 species) and forest (26.46 ± 1.34 species) but the two differed significantly from that of the mixed-crop field (19.22 ± 0.63 species). The complete list of ant species is displayed in Annex 1.

Species richness was also affected by season ($F_{(5,75)} = 2.51$; P = 0.04), but its interaction with vegetation type was not significant season ($F_{(10,70)} = 1.00$; P = 0.45). Average species richness was also higher in the short dry season SD (28.92±2.03 species) followed by the short wet season SW07 (26.13 ± 2.31 species), the long wet season LW (23.54 ± 1.73 species), the long dry season LD08 (23.37 ± 1.88 species), the short wet season SW08 (22.50 ± 0.86 species)

and the long dry season LD07 (21.53 ± 1.12 species) (Figure 2A). Species richness during the long short dry season SD differed significantly from that of the short wet season SW08, the long wet season LW, the long dry seasons LD08 and LD07. Species richness was not affected by any of the four PCA axes.

Species abundance (Total occurrence of a species)

Species abundance was not affected by vegetation ($F_{(2,78)} = 2.31$; $P = 0.11$). However, abundance in the fallow (30.21 ± 1.20) was higher compared to mixed-crop field (28.84 ± 1.42) and forest (25.98 ± 1.41).

Species abundance was affected by season ($F_{(5,75)} = 3.07$; $P = 0.02$) and the interaction between vegetation and the first PCA axis ($F_{(2,78)} = 3.33$; $P = 0.04$). Average abundance during the short wet season LW (31.17 ± 1.36) was higher compared to that of the long dry season LD08 (30.40±2.16), the short dry season SD (30.12 ± 2.12), the short wet season SW07 (29.53±2.66), the long wet season SW08 (25.92 ± 1.52) and the long dry season LD07 (24.08 ± 1.12 species) (Figure 2B). A positive correlation was found between species richness and species abundance ($r = 0.45$; $P < 0.0001$; $n = 81$). This correlation was more significant when analysis was done by vegetation type except in the mixed-crop field: fallow ($r = 0.48$; $P < 0.0001$; $n = 27$); forest ($r = 0.88$; $P < 0.0001$; $n = 27$); mixed-crop field ($r = 0.25$; $P = 0. 28$; $n = 27$).

Species density (number of species/m^2)

Species density was affected by season ($F_{(5,75)} = 4.84$; $P = 0.01$), the third PCA axis ($F_{(1,79)} = 4.23$; $P = 0.04$) and the interaction between vegetation and the third PCA axis ($F_{(2,78)}=3.37$; $P = 0.04$) (Table 2). Average species density in the fallow (3.99 ± 0.20 species/m^2) was higher compared to that of the mixed-crop field (3.20 ± 0.15 species/m^2). It was also significantly higher compared to that of the forest (3.38 ± 0.20 species/m^2). Density in mixed-crop field and forest did not significantly differ from each other.

Average species density during the long wet season (LW) (4.33 ± 0.18 species/m^2) did not differ significantly from that of the short dry season SD (4.10 ± 0.36 species/m^2), but was higher compared to the densities observed during the long dry season LD08 (3.54 ± 0.24 species/m^2), the short wet season SW07 (3.53 ± 0.35 species/m^2), the short wet season SW08 (3.01 ± 0.15 species/m^2) and the long dry season LD07 which had the lowest species density

46

$(2.92 \pm 0.17$ species/m^2). No significant difference was observed between densities during the long dry season LD07 and the short wet season SW08, the short wet season SW07 and the short wet season SW08 (Figure 2C).

Species density was significantly correlated with species richness ($r^2 = 0.64$, P < 0.0001; n = 81) and species abundance ($r^2 = 0.83$, P < 0.0001; n = 81)

Table 2: Analysis of the effect of vegetation type, season and their interaction on species richness, species abundance, species density, species activity (Log-transformed), and ant species composition (df = degree of freedom, MS = Mean of square, F = F statistic, p = probability associated to F. Only PCA axes with significant difference are presented for each parameter.

Variables	DF	MS	F	P
Species richness				
Vegetation	2	181.27	9.21	0.0004
Season	5	49.27	2.51	0.04
Species abundance				
Prin1*vegetation	2	96.39	3.33	0.04
Season	5	88.72	3.07	0.02
Species density				
Season	5	2.65	4.84	0.001
Prin3	1	2.31	4.23	0.04
Vegetation * Prin3	2	1.84	3.37	0.04
Species activity (Log)				
Vegetation	2	2.01	4.54	0.01
Season	5	1.13	2.55	0.04
Prin1	10	2.49	5.61	0.02
Species composition				
Vegetation	2	1.14	16.43	0.0001
Season	5	0.26	3.69	0.005
Vegetation * Season	10	0.25	3.64	0.001

Note: Prin1 is the measure of air and soil temperature. Prin3 is the measure on soil pH, organic matter, total nitrogen, air humidity and the ratio C/N

Species activity (Total number of individuals captured with pitfall traps)

The total number of individual (log-transformed) captured in pitfall trap was affected by vegetation ($F_{(2,78)}$ = 4.54; P = 0.01), season ($F_{(5,75)}$ = 2.55; P = 0.04) and the first PCA axis ($F_{(1,79)}$ = 5.61; P = 0.02**).** The interaction between vegetation type and season was not significant ($F_{(10,70)}$ = 0.68; P = 0.73**)** (Table 2). Average species activity in the mixed-crop field (2.66 ± 0.13 individuals) was higher than in the fallow (2.36 ± 0.15 individuals) and forest (2.12 ± 0.16 individuals). However significant difference was observed only between mixed-crop field and forest.

There was no significant difference in species activity between the long wet season LW (2.80 ± 0.25 individuals) and the long dry season LD08 (2.69±0.25 individuals) and between the short dry season SD (2.51 ± 0.21 individuals) and the long dry season LD07 (2.24 ± 0.16 individuals). Activity during these seasons was however greater than that observed during the short wet seasons SW07 (2.08 ± 0.17 individuals) and SW08 (2.01 ± 0.18 individuals). The two later were not significantly different (Figure 2D).

Species activity was positively correlated with species density (r^2 = 0.37, P = 0.0006; n = 81) and species abundance (r^2 = 0.55, P < 0.0001; n=81)

Composition of ant assemblage

The composition of ant assemblage was affected by the vegetation ($F_{(2,251)}$ = 16.43, P = 0.0001); season ($F_{(5,248)}$ = 3.69, P = 0.005) and the interaction between the two factors also have a significant effect ($F_{(10,243)}$ = 3.64, P = 0.001) (Table 2).

Overall, difference in ant composition was observed between forest and mixed-crop field (t = 2.38, P = 0.01) and between forest and fallow, (t = 5.17, P = 0.01). The differences were observed during the long dry season LD07 and LD08, the short dry season SD and the short wet season SW08. Significant differences in ant composition were found between fallow and mixed-crop field during the short dry season SD (t = 3.25, P = 0.04) and the short wet season SW08 (t = 6.64, P = 0.03) (Table 3).

Difference in species composition between seasons was observed in the mixed-crop field and in the fallow. No seasonal variation in species composition was observed in the forest (Table 4).

48
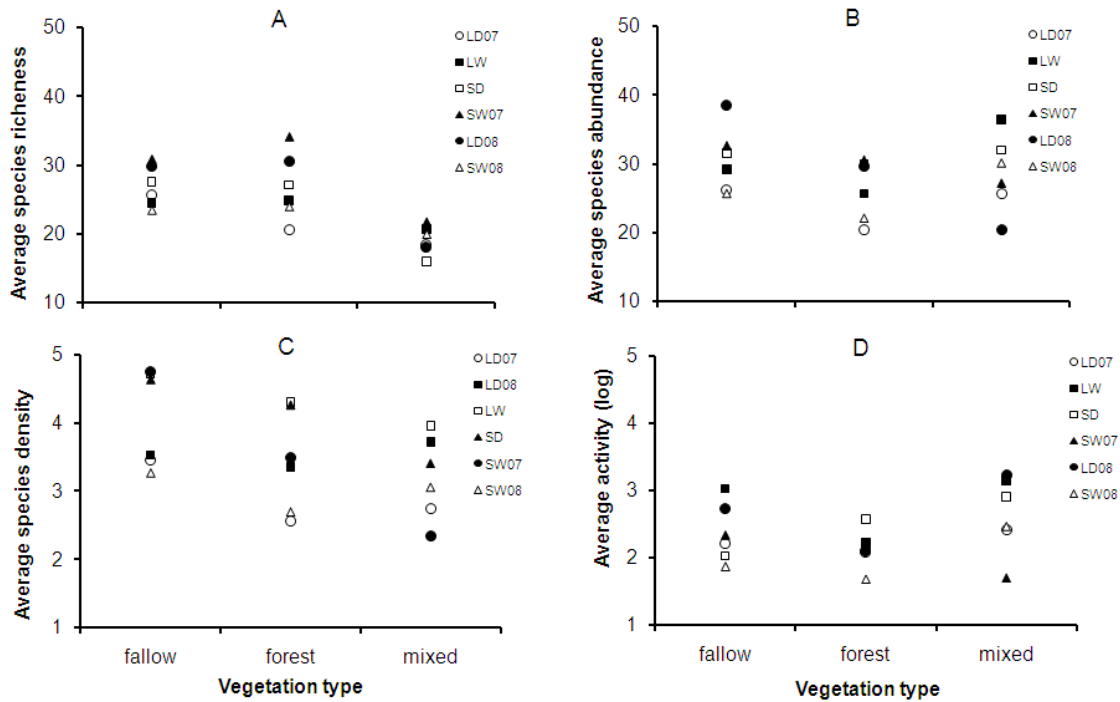
Fig. 2 Average species richness (A), species abundance (B), species density (C) and species activity (D) ant density in the three vegetation types during the short wet season (SW07) ; the short dry season (SD07); the long wet season on (LW07); the long dry season (LD07); the long dry season (LD08) and the short wet season (SW08)

Table 3: Pair-wise *a posteriori* comparison of ant composition assemblage among vegetation type within seasons and among seasons within vegetation type using the permutation calculated t-statistic (numbers in table). Details are given only for seasons with significant difference in at least one vegetation type. [*] indicates significant difference ($P < 0.05$). LD07 = long dry season 2007; LD08 = long dry season 2008; SW08 = short wet season 2008; SD = short dry season.

Within seasons	LD07	LD08	SD	SW08	All seasons
Fallow-Forest	2.81	4.33[*]	1.99	4.12	5.17[*]
Fallow-Mixed	0.30	0.85	3.25[*]	6.64[*]	1.91
Forest-mixed	2.65[*]	2.36	1.53	10.98[*]	2.38[*]

Table 4: Pair-wise *a posteriori* comparison of ant composition assemblage among seasons within vegetation type using the permutation calculated t-statistic (numbers in table). Details are given only for seasons with significant difference in at least one vegetation type. [*] indicates significant difference (p< 0.05). For season abbreviations see rainfall pattern.

Within vegetation types	Fallow	Forest	Mixed	All vegetation
LD08-SW07	2.73[*]	0.02	2.53[*]	2.60[*]
LD08-SW08	5.79[*]	0.32	0.74	0.70
LD08-SD	2.78	0.46	4.07	3.02[*]
LD07-SD	1.38	1.14	4.58[*]	1.02
LW-SW08	2.41	0.30	4.02[*]	0.91
SD-SW08	0.09	0.27	6.91[*]	2.51[*]
SW07-SW08	0.61	0.37	4.38[*]	2.03

Effect of vegetation type and abiotic factors on Anoplolepis tenella

A. tenella abundance

A. *tenella* abundance was affected by vegetation ($F_{(2,78)} = 10.72$, *P* =0.0001). It was more abundant in the mixed-crop field (16.81±2.83) compared to fallow (10.44±1.86) and forest (8.00 ± 1.42) (Figure 4). It was also affected by the first PCA axis Prin 1 ($F_{(1,79)}$=35.70; *P* < 0.0001), the third axis Prin3 ($F_{(1,79)} = 9.11$; *P* = 0.004) and the interaction between vegetation type and the first PCA axis ($F_{(2,78)} = 4.19$; *P* = 0.02) (Table 5). There were no significant differences in *A. tenella* occurrence in Awae and Matomb. However the two locations differed significantly from the lowland area Boga and Sombo ($F_{(3,77)} = 16.21$, *P* <0.0001).

Season did not affect *A. tenella* abundance ($F_{(5,75)} = 1.23$, *P* = 0.31), neither did its interaction with vegetation type ($F_{(10,70)} = 1.66$, *P* = 0.11). However, highest abundance was recorded during the short dry season SD (14.25 ± 4.00) followed by the long wet season LW (13.08 ± 3.57), the short wet season LD08 (12.27 ± 3.21) and the short wet season SW07 (11.08 ± 2.75). The lowest abundance was recorded during the short wet season LD07 (9.27 ± 2.97).

A. *tenella* abundance was positively correlated with ant species density (r = 0.25; n = 81, *P* = 0.02).

A. tenella density

A. *tenella* density was affected by vegetation type ($F_{(2,78)} = 5.35$, $P = 0.008$). It was higher in the mixed-crop field (2.16 ± 0.48 individual/m^2) than in the fallow (1.11 ± 0.27 individual/m^2) and forest (0.75 ± 0.18 individual/m^2). It was also affected by the first PCA axis Prin1 ($F_{(1,80)} = 10.33$, $P = 0.002$). Season didn't affect A. *tenella* density ($F_{(5,75)} = 1.88$, $P = 0.11$), neither did its interaction with vegetation type ($F_{(10,70)} = 1.89$, $P = 0.07$). However, highest density was recorded during the short dry season SD (2.19 ± 0.84 individual/m^2) followed by the short wet season SW07 (1.55 ± 0.48), the long dry season LD08 (1.51 ± 0.54 individual/m^2), the long wet season LW (1.22 ± 0.41 individual/m^2) and the long wet season SW08 (1.08 ± 0.31 individual/m^2). The lowest density was recorded during the long dry season LD07 (0.69 ± 0.29).

A. *tenella* density was positively correlated with ant species density ($r = 0.29$; $n = 81$, $P = 0.009$) and species activity ($r = 0.25$; $n = 81$, $P = 0.03$).

Table 5: Analysis of the effect of vegetation type, season and their interaction on *Anoplolepis tenella* abundance, density and activity (df = degree of freedom, MS = Mean square, F = F statistic, *P* = probability associated to F). Only PCA axes with significant difference are presented for each parameter.

Variables	DF	MS	F	*P*
A. tenella **abundance**				
Vegetation	2	476.15	10.72	0.0001
Season	5	54.67	1.23	0.31
Prin1	1	1586.27	35.70	<0.0001
Vegetation * Prin1	2	186.07	4.19	0.02
A. tenella **density**				
Vegetation	2	9.32	5.35	0.008
Season	5	3.28	1.88	0.11
Vegetation * Season	10	3.28	1.89	0.07
Prin 1	1	17.99	10.33	0.002

Variables	DF	MS	F	P
A. tenella activity				
Vegetation	2	10.33	9.43	0.0003
Season	5	2.64	2.41	0.04
Vegetation * Season	10	3.01	2.72	0.006
Prin1	1	35.33	32.28	<0.0001
Prin3	1	7.45	6.81	0.04
Prin1*Vegetation	2	6.51	5.95	0.005

Note: Prin1 is the measure of air and soil temperature. Prin3 is the measure on soil pH, organic matter, total nitrogen, air humidity and the ratio C/N

A. tenella activity

Mean *A. tenella* activity (log-transformed) was affected by vegetation type ($F_{(2,79)} = 9.43$, $P = 0.0003$) and its interaction with the first PCA axis ($F_{(2,79)} = 5.95$, $P = 0.005$), the first PCA axis ($F_{(1,80)} = 32.28$; $P < 0.0001$) and also the third axis ($F_{(1,80)} = 6.81$; $P = 0.004$). The activity was higher in the mixed-crop field (2.46 ± 0.40 individuals) compared to fallow (1.63 ± 0.29 individuals) and forest (1.36 ± 0.24 individuals). Activity in the fallow did not significantly differ from that observed in the forest.

Season had a significant effect on *A. tenella* activity ($F_{(5,75)} = 2.41$, $P = 0.04$), and so did its interaction with vegetation type ($F_{(10,70)} = 2.75$, $P = 0.009$). Activity during the long dry season LD08 (2.32 ± 0.54 individuals) was not significantly different from that of the short dry SD (2.15 ± 0.55 individuals). However these two significantly differed from the other seasons. Lowest activity was recorded during the long dry season LD07 (1.39 ± 0.42).

A. tenella activity was positively correlated with ant species density ($r = 0.23$; $n = 81$; $P = 0.04$).

Discussion

There are few studies that focus of seasonal variations and microclimatic factors affecting species richness, abundance, density and activity in tropical ant communities. It has been shown that moisture and wet season increase species activity and density (Kaspari et al., 2000). Overall,

ant parameters were higher during the dry season although the difference with the wet season was not significant. This pattern was also observed in southeast Cameroon (Deblauwe and Dekoninck, 2007b). Significant seasonal variation was found in ant activity with lowest activity of species like *A. tenella* recorded during the short wet season SW07 in the mixed-crop field. This period correspond to the first sampling and significant changes were made in mixed-crop with vegetation burning with and cassava plants at one month after planting. At this stage, scale infestation on cassava is very low (Hanna, unpublished). When there is seasonal variation in species activity, it is thought to follow species density (Levings and Windsor, 1984). This hypothesis was verified in our study. These seasonal variations can be related to microclimatic conditions since ant parameter could be predicted by some axes from the principal component analysis of abiotic factors (climate and soil). Soil attributes are known to influence ant diversity. Ant abundance and diversity were shown to decrease with increasing altitude and soil moisture. Furthermore, clay-rich soils can affect ant queen mass and therefore their distribution (Johnson, 2000). Survivorship in *Pogonomyrmex rugosus* (Emery) and *Pogonomyrmex barbatus* (Smith) alates was associated to soil with higher moisture retention. However, clay soil also could indirectly affect ants by impacting plant distributions (Boulton et al., 2005). Abundant species like *A. tenella* exhibited some associations with soil properties. Its density and activity was affected by soil and air temperature (Prin1), soil organic matter, soil organic C and total N and air relative humidity (prin3).

The type of vegetation had more pronounced effect on ant species richness, activity and density compared to season. Species richness in the mixed-crop field was significantly lower compared to that of the forest. The difference, however, was not as pronounced as presented in other studies, where species richness in disturbed areas was less that the half of that recorded in undisturbed areas (MacKay et al., 1991; Roth et al., 1994; Nepstad et al., 1995; Vasconcelos, 1999). This low difference can be attributed to the contiguity of the different vegetation types which displays a mosaic pattern. Mixed-crop fields are always surrounded by a fallow or a forest, and generalist ant species which can nest in several sites or use a broad range of foods items can be found in both vegetations (MacKay et al., 1991). However, some species were restricted to specific vegetation with the highest number of restricted species (45 species) found in the forest and the lowest in the mixed-crop fields (8 species).

In addition, the age, structure and plant composition forest could be quite different from those in other study, thus accounting for the lower difference between natural and anthropogenic sampling sites. Habitat-associated ant assemblages comprise species adapted to the microclimate within their particular habitat (Fisher and Robertson, 2002) or species with narrow or specialized feeding or nesting habits, hence, some species can be recorded only in a specific vegetation type. However, each vegetation type could share more than a hundred species with others.

The difference in species richness density and activity can also be attributed to structural difference between our sampling sites. Some studies have shown that disturbance affects ant assemblages by altering shade regimes (King et al., 1988; Hoffmann et al., 2000), vegetation structure (Greenslade and Greenslade, 1977) and plant species richness (Hoffmann and Andersen, 2003). Trees for example reduce the amount of water and light reaching the soil surface (Belsky and Amundson, 1992; Fisher and Robertson, 2002). In our study, shade regimes and vegetation structure were all altered during the conversion of forest to farmland. As a consequence, microclimatic factors were not the same in all the vegetation type. Soil and air temperature for example were always higher in the mixed-crop fields compared to fallow and forest whereas air humidity was always low during the day. This difference in environmental factors between habitats may affect the occurrence and diversity of ant species (Fisher and Robertson, 2002).

Ant activity and density was also dependent on habitat type and seasons, and their interaction was also significant. Observed temporal changes in activity and density can be related to environmental disparities between the sampling periods. Ant species may respond differently to climatic change depending on their physiological tolerance levels, ecological requirement and competitive ability (Deblauwe and Dekoninck, 2007b; Barrow and Parr, 2008). There are three niche factors that may affect their distribution and activity: space, food type and time (Schoener, 1974; Albrecht and Gotelli, 2001). Most competitive species, through their numerical dominance, may partly control the distribution of competitively inferior species. Therefore the density and abundance of the subordinate species are lower in the presence of its competitors, which for example monopolize food resources (nectaries or honeydew-producing homoptera aggregations) (Bluethgen et al., 2000)

We found a significant and positive correlation between species richness and species abundance, especially in the forest, supporting the "more individual hypothesis" (Clarke and

Gaston, 2006). This theory was also verified in Andean moth (Beck et al., 2010). According to this hypothesis, the availability of a resource results in greater diversity of organized that consumes it. We found in another study that plant offering nectar or hosting Hemipteran were more frequent in the forest compared to fallow and mixed-crop field, thus justifying its greater species richness (Fotso Kuate et al., in prep).

Anoplolepis tenella was more abundant in the mixed-crop field and fallow than any other ant species. It was also most abundant in the upland compared to lowland area. At least two explanations for the abundance of *A. tenella* are worth considering. First, most of *A. tenella* nests are found in the mixed-crop field under crop plants mainly cassava and cocoyam or in fallow under abandoned cassava plants (Fotso Kuate et al., 2006). This nesting behavior is related to its association with sap-sucking *Stictococcus vayssierei* (Hemiptera, Stictococcidae) which infest several cultivated plants. The abundance of these host plants in mixed-crop field positively affects the abundance of *A. tenella* and enhance its competitive ability, hence it higher density and activity. A second explanation could come from environmental factors such as soil and air temperature and air humidity. This explanation is supported by the PCA axes from the abiotic parameters. The disparities of these abiotic factors between upland and lowland area might affect *A. tenella* competitiveness especially in the lowland areas where it is either absent or rare and where coincidently *S. vayssierei* is also absent.

In conclusion, ant species richness, abundance, activity and density are driven by vegetation type and the observed differences can be postulated to be linked to environmental disparities between these vegetation types.

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Chapter 3: Interaction between ants, plants and honeydew-producers in the humid forest zone of southern Cameroon

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Running title: Ant-plants-hemipteran interaction in southern Cameroon

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Summary

Extrafloral nectaries and hemipteran honeydew are often discussed as two alternative mechanisms encouraging ant visitation in mutualistic ant-plant relationships, but little is known about the processes that generate distribution pattern in species-rich insect communities. The richness of ants, plants with extrafloral nectaries and hemipteran and their interactions was investigated in three vegetation type of southern Cameroon (mixed-crop field, fallow and forest). Sampling was conducted in these vegetations during the wet and the dry seasons in five locations. Results showed that partitioning of ant species between season and vegetation was significantly different from random. High specialization index was observed in hemipteran/plants and ant/hemipteran interactions. Low specialization index was observed between ant and plant producing extrafloral nectaries, mainly in the mixed-crop field. Ant species were mostly found in non-aggressive co-occurrence at nectar and honeydew sources. At the species level, specialization index was high for *Anoplolepis tenella* (0.86 ± 0.06) and also for its associated hemipteran (0.97 ± 0.02). These results outline the effect of vegetation, food source and spatio-temporal pattern on the structure of the ant assemblage in southern Cameroon.

Key words: *Anoplolepis tenella*, Extrafloral nectaries, Honeydew, Season, Specialization index, *Stictococcus vayssierei*, Vegetation.

INTRODUCTION

A central question in ecology concerns the determinants of community structure. Despite great progress, a synthetic model of the causes of patterns of distribution, abundance, diversity, size structure, and spatial patterns remains elusive (Menge et al. 2002). Plant and animal communities are shaped by several interacting processes. Some of these processes can reduce the fitness of a species through predation (top-down effects) or generate suitable conditions that favor the proliferation of a species (bottom-up effects). The later can be perceptible through resource availability (Hunter and Price 1992). Niche differentiation and reduction in interspecific competition can also account for high diversity of species that are resource consumers (Armbrecht et al. 2004).

Ant assemblages have been the focus of many studies, because of their extraordinary abundance and primary ecological function (Hölldobler and Wilson 1990) and hence economic importance (Way and Khoo 1992). Species richness of ant assemblage attracted to food rewards varies geographically, seasonally (Rico-Gray et al. 1998) and between day and night (Hossaert-McKey et al. 2001). In *Triumfetta semitriloba* Jacq., the quantity or quality of EFN secretion is considered to dominate over extrinsic factors in determining ant visitation and its effects (Sobrinho et al. 2002). *Macaranga tanarius* (L.) Müll.Arg. plants treated with jasmonic acid to increase EFN secretion showed a significant increase in ant activity over a period of 24 hours (Heil and McKey 2003).

EFNs have been reported from over 90 families of flowering plants and ferns (Koptur 1992), mostly from tropical and subtropical regions. There is considerable variation in EFN morphology and visitor spectra of ants among other insects (Oliveira and Brandão 1991). Associations of ants and hemipteran, on the other hand, occur in many if not on all flowering plant families and are widespread from tropical to temperate habitats (Buckley 1987; Way 1963). Many different hemipteran species are ant-tended, and a high level of ecological, morphological, and behavioural variation in both ants and hemipteran accompanies this relationship (Fagundes et al. 2005; Mckey et al. 2005; Oliveira and Del-Claro 2005). Although EFNs and hemipteran honeydew have been discussed as two alternative mechanisms encouraging ant visitation on plants, little is known about the processes that generate distribution pattern in species-rich insect communities. Moreover, intensive studies have been restricted to forest and orchards and few studies have compared the distribution of both interaction types on different plant species and vegetation type.

The objective of our study was to evaluate the relationship between ant species composition and plants with EFNs or hemipteran in mixed-crop field, fallow and forest, which are the three most common vegetation types in southern Cameroon. Specifically, we (1) compared the species spectra of ants attending EFNs and hemipteran, (2) measured co-occurrence of ant species on plants offering EFNs or honeydew, and (3) looked for preferences between associations of ant, plant, and hemipteran taxa in these vegetations. Emphasis was laid on the association between *Anoplolepis tenella* Santschi (Hymenoptera; Formicidae) and the African root and tuber scale *Stictococcus vayssierei* Richard (Hemiptera; Stictococcidae), a pest that infest several crop with greatest occurrence on cassava in central Africa.

MATERIAL AND METHODS

Study area

Sampling was conducted from July 2007 to February 2008 in four locations in southern Cameroon, i.e. Awae II (03°35'37"N; 011°36'40"E), Matomb (03°48'11"N; 011°03'27"E), Boga (03°53'15"N; 010°46'25"E) and Sombo (03°53'36"N; 010°42'26"E). Two zones were selected in Awae II giving a total of five sampling zones. The climate is equatorial, with a bimodal rainfall distribution, and four distinct seasons: two humid seasons corresponding to two cropping seasons: mid August to mid November and March to June, and two dry seasons from mid November to February and from July to mid-August. Annual rainfall is 1500 to 2000 mm and the mean annual temperature is 25°C; mean daily temperature ranges from 19.2 to 28.6 °C. The vegetation in southern Cameroon is composite and seven classes of land uses can be identified including slash-and-burn dominant farmlands (also refer as mixed-crop field), *Chromolaena odorata* dominant short-fallows, long-fallows or regenerated forests (Thenkabail 1999).

Sampling methods

Four sampling events were conducted in each of the three vegetation types (mixed-crop field, fallow and forest), two in the course of the wet season (June 2007 and October 2007) and two during the dry season (December 2007 and February 2008). Each vegetation type was replicated twice in each of the five sampling zones. Two parallel transect lines 50-m long and 10–m apart were delimited each plot and five sampling points were selected at a constant 10-m interval on each transect.

Sampling method was adapted from the literature (Bluethgen et al. 2004b; Bluethgen et al. 2006; Bluethgen et al. 2007). In the forest, sampling was conducted on small plants (maximum height 2 m) and on plants with small diameter which could be easily bent to reach their upper canopy. Sampling was carried out during daytime. On each plant, we randomly selected five twigs from each branch, and noted the presence of hemipteran and ants. For hemipteran, different developmental stages were collected by cutting the infested part (roots/tubers or fruits) and crawlers were removed using a brush. Ant species were collected either directly from the honeydew or nectar source using an aspirator. For fast moving ant species, infested twigs were beaten above a basin (Diameter: 40cm, depth: 15 cm) and then ants were collected with the mouth aspirator. Potential host plants of *S. vayssierei* were uprooted and

inspected for the presence of the scale. Samples were preserved in 70% ethanol for identification in the laboratory. Ant species were sorted to genus using taxonomic literature (Bolton 1994) and the online ant resource database (Taylor 2010). Species within a genus were sorted based of external morphology (morphospecies). Hemipteran were also sorted to morphospecies and grouped into families. *Stictococcus vayssierei* was reported separately from its family (Stictococcidae) to highlight its interaction with its associated ants and host plant.

In addition to hemipteran sampling, we surveyed additional plants for extrafloral and floral nectaries. The surveys included plant species known to provide nectar, but also novel cases where ant activity attracted our attention to these sources. Plants that could not be directly identified in the field were collected, hard-pressed, dried and identified by the Cameroon National Herbarium. For each host plant, we collected ant species when they consumed nectar in the observable area of these plants, typically including the entire foliage on small under-storey shrubs and entire inflorescences, but often only accessible and exposed parts of the tree climbing plants.

Data analysis

For the analysis of associations between ants and plants, ants and hemipteran insects, contingency tables of ant species *vs.* plant species and ant species *vs.* hemipteran species were used with frequencies of interactions as cell entries (Bluethgen et al. 2004a).

We used the incidence-based index Chao2 to estimate the expected species pool in a complete sampling (Colwell and Coddington 1994). This analysis were done with EstimateS v.8.0 software (Colwell et al. 2006)

Species partitioning between hemipteran, ant and plant associations was analyzed using a two-dimensional entropy across the matrix, $H = -\sum_i \sum_j (p_{ij} \log p_{ij})$, was calculated based on the contingency tables of observed association (Bluethgen et al. 2006). The strength of species partitioning was calculated as $H_2' = (H - H_{min})/(H_{max} - H_{min})$, where H_{max} and H_{min} are the largest and smallest possible entropy, respectively, for matrices with the same row and column totals. Hence, H_2' ranges between zero (for a random distribution) and one (for the maximum degree of partitioning) (Bluethgen et al. 2006). H_2' analysis was done for each sampling site because by pooling data into a single large network, many ant species will only occur in a certain site, some plant or hemipteran species only in other sites, and they could never potentially interact. H_2' was

therefore expressed as mean ± sd across sampling sites for each vegetation type. The following matrices were used: ant/(E)FN, ant/honeydew-plant, ant/hemipteran and hemipteran/plant networks. Analysis was performed using an algorithm based on the matrix statistic (program available at http://rxc.sys-bio.net/).

Species co-occurrence

The number of ant species that foraged simultaneously on the same resource type on the same plant individual was counted and denoted as S. Ant species co-occurrence was defined as the proportion of plant surveyed where S>1. The proportion of visits with co-occurrences was calculated only when a minimum of two ant workers of each species were present on the same plant.

RESULTS

Structure of ant assemblage

In total, 99 ant species were recorded - 62 species foraged for nectar and honeydew, 25 species were recorded only on nectar, and 12 species only on honeydew (Annex 2). Estimated ant species richness (± sd) was 121.3 (± 15.6) on nectaries and 88.2 (± 8.2) on honeydew sources (EstimateS; Chao2, 2000 runs). Records of ants on nectaries and honeydew represented respectively 70.7 % and 82.9 % of the expected ant species.

Thirty four ant species were found in mixed-crop field, 62 in the fallow and 67 in the forest (estimated ant species richness (± sd): 78.1 (± 28.3), 82.5 (± 11.6) and 85.2 (± 9.8) respectively). Partitioning of ant species between the three vegetation type was significantly different from random (H_2' = 0.54 ± 0.01). Eighty six species were recorded during the rainy season and 57 during the dry season. The partitioning of ant species between the two seasons was significantly different from random (H_2' = 0.27 ± 0.03).

Extrafloral and floral nectaries

Thirty seven plant species with active EFN were observed in the study (Table 1). Flower nectar use by ants was recorded on 7 plant species. The distribution of EFN and FN plants

differed significantly between the three vegetation type (Pearson $\chi^2 = 468.04$, df = 76, p<0.0001). Most of the host plants were found in the forest and less in the mixed-crop fields (Figure 1).
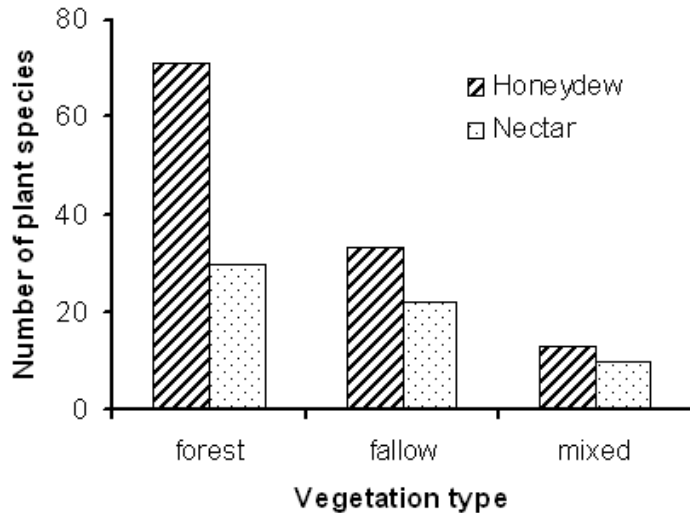
Fig. 1 Distribution of plants hosting hemipteran or offering nectar (EFN or FN) in the three vegetation types. Comparison between vegetation: nectar $\chi^2 = 468.04$, df = 76, P < 0.0001; honeydew: $\chi^2 = 564.2$, df = 44, P < 0.0001.

Fifteen plant species offering nectar presented 2 or more interactions with 34 ant species. Association between ant and plant with (E)FN was different from random in the three vegetation type: fallow ($H'_2 = 0.14 \pm 0.02$); forest ($H'_2 = 0.28 \pm 0.14$); mixed-crop field ($H'_2 = 0.20 \pm 0.10$). Ant species can be considered as weakly partitioned across plant species because the specialization is low, especially in the fallow. Overlap between plants species used was common, and ant species visited two or more nectar plants (Table 1).

Table 1: Plant species with (a) extrafloral nectaries and (b) floral nectaries visited by ants. Number represents count of plant individuals with positive observations of ant visits.

Family	Plant species	Fallow	Forest	Mixed	Total
a) Extrafloral nectaries					
Apocynaceae	*Funtumia elastica* Stapf	0	2	0	2
Bignoniaceae	*Newbouldia laevis* Seem.	1	5	2	8
Burseraceae	*Dacryodes edulis* (G.Don) H.J.Lam	0	1	0	1
Caesalipiniaceae	*Cassia hirsuta* L.	7	0	0	7
	Dialium pachyphyllum Harms	0	1	0	1
Costaceae	*Costus afer* Ker Gawl.	51	9	0	60
Cucurbitaceae	*Momordica cabraei* (Cogn.) Jeffrey	0	2	0	2
	Zehneria sp.	2	0	1	3
Dichapetalaceae	*Dichapetalum sp.*	2	2	0	4
Euphorbiaceae	*Alchornea cordifolia* Müll.Arg.	91	17	26	134
	Macaranga assas Amougou	15	25	0	40
	Mallotus oppositifolius Müll.Arg.	0	45	0	45
	Manniophyton fulvum Müll.Arg.	9	3	0	12
	Phyllanthus discoideus Müll.Arg.	2	0	1	3
Fabaceae	*Pueraria phaseoloides* Benth.	7	0	1	8
Leeaceae	*Leea guineensis* G.Don	0	2	0	2
Loganiaceae	*Anthocleista* sp.	0	2	0	2
Malvaceae	*Urena lobata* Linn.	5	0	4	9
Marantaceae	*Haumania danckelmaniana* (J.Braun & K.Schum.) Milne-Redh.	18	57	3	78
	Hypselodelphys zenkeriana K.Schum.	0	8	0	8
	Marantochloa sp.	0	3	0	3
Meliaceae	*Carapa grandiflora* Sprague	1	3	0	4
	Carapa parviflora Harms	0	4	0	4
	Carapa sp.	0	3	0	3
Mimosaceae	*Albizia gummifera* C.A.Sm.	1	9	0	10

Family	Plant species	Fallow	Forest	Mixed	Total
Mimosaceae	*Albizia zygia* J.F.Macbr.	44	11	14	69
Moraceae	*Ficus exasperata* Vahl	5	0	1	6
Ochnaceae	*Lophira alata* Banks ex C.F.Gaertn.	0	1	0	1
Passifloraceae	*Adenia sp.*	4	0	0	4
Polygalaceae	*Carpolobia lutea* G.Don	2	1	0	3
Rubiaceae	*Bertiera sp.*	0	1	0	1
	Leptactina arnoldiana De Wild.	0	2	0	2
	Morinda lucida Benth.	3	0	0	3
Rutaceae	*Fagara macrophylla* (Oliv.) Engl.	0	2	0	2
Sapindaceae	*Allophyllus africanus* P.Beauv.	0	1	0	1
Ulmaceae	*Celtis zenkeri* Engl.	0	1	0	1
Verbenaceae	*Clerodendron dusenii* Gurke	6	0	1	7
b) Floral nectaries					
Caesalipiniaceae	*Cassia hirsuta* L.	7	0	0	7
Commelinaceae	*Palisota hirsuta* K.Schum.	1	8	0	9
Connaraceae	*Cnestis ferruginea* DC.	3	0	0	3
Costaceae	*Costus afer* Ker Gawl.	51	8	0	59
Leeaceae	*Leea guineensis* G.Don	0	2	0	2
Malvaceae	*Urena lobata* Linn.	5	0	4	9
Verbenaceae	*Clerodendron dusenii* Gurke	5	0	1	6

Six ant species (*Camponotus acvapimensis*, *Tetraponera lepida*, *Camponotus brutus*, *Polyrhachis laboriosa*, *Crematogaster gabonensis* and *Crematogaster stadelmanni*) showed a significantly greater presence at nectar sources in the fallow and four species (*Technomyrmex lujae*, *Tetramorium magnificum*, *Odontomachus troglodytes*, *Technomyrmex kohli* were significantly more common in the forest (Table 1).

All the ants species recorded on FNs were also recorded on ENFs but we found a separation of ant species that were involved in honeydew collection and those collecting nectar (Pearson $\chi^2 = 298.1$, df = 28, ($P < 0.0001$)

Honeydew

We recorded 44 hemipteran on 93 plant species. Represented groups were Aphididae (10 morphospecies), Membracidae (7 morphospecies), Pseudococcidae (7 morphospecies) Coccidae (19 morphospecies) and Stictococcidae (2 morphospecies). Thirty one hemipteran morphospecies grouped into five families had three or more interactions with 24 plant species and are presented in table 2.

Table 2. Distribution of hemipteran species and their host plant in the three vegetation type (only species with a total of 3 or more interactions with plants are presented in the table).

Hemipteran	Host Plants	Fallow	Forest	Mixed
Aphididae	*Chromolaena odorata* (L.) R.M.King & H.Rob.	35	0	12
	Zea mays L.	0	0	24
	Triumfetta cordifolia Sessé & Moc.	3	0	0
Pseudococcidae	*Chromolaena odorata* (L.) R.M.King & H.Rob.	3	0	0
	Saccharum officinarum L.	3	0	0
	Urena lobata Linn.	3	0	0
	Triumfetta cordifolia Sessé & Moc.	3	0	0
	Cnestis ferruginea DC.	3	0	0
	Haumania danckelmaniana (J.Braun & K.Schum.) Milne-Redh.	0	13	0
	Saccharum officinarum L.	3	0	0
Membracidae	*Alchornea cordifolia* Müll.Arg.	8	1	2
	Macaranga assas Amougou	3	5	0
	Triumfetta cordifolia Sessé & Moc.	34	2	3
	Mallotus oppositifolius Müll.Arg.	0	4	0
Coccidae	*Chasmanthera dependens* Hocht.	2	2	0
	Haumania danckelmaniana (J.Braun & K.Schum.) Milne-Redh.	0	3	0
	Belonophora werhamii Hutch. & Dalz.	0	3	0
	Caloncoba welwitchii (Oliv.) Gilg.	1	2	0
	Costus afer Ker Gawl.	4	2	0

Hemipteran	Host Plants	Fallow	Forest	Mixed
	Pierrina zenkeri Engl.	0	3	0
	Carapa grandiflora Sprague	0	3	0
	Diospyros crassiflora Hiern	0	3	0
Stictococcidae	*Aleurite sp.*	0	3	0
	Costus afer Ker Gawl.	6	3	0
	Macaranga assas Amougou	2	1	0
	Myrianthus arboreus Beauv.	0	2	1
	Uapaca guineensis Müll.Arg.	0	4	0
Stictococcus vayssierei	*Aframomum daniellii* K.Schum.	2	2	0
	Arachis hypogaea L.	0	0	31
	Manihot esculenta Crantz	29	0	95
	Xanthosoma mafafa Schott.	1	0	20
Grand Total		148	61	188

Association between plant and hemipteran was different from random in the three vegetation type and maximum level of specialization was observed in the mixed-crop field: fallow ($H'_2 = 0.78 \pm 0.07$); forest ($H'_2 = 0.52 \pm 0.19$); mixed-crop field ($H'_2 = 1.00 \pm 0.00$). The distribution of hemipteran host plants differed significantly between the three vegetation type (Pearson $\chi^2 = 564.2$, df = 44, $P < 0.0001$) (Figure 1). Most of the host plants that had many interactions with honeydew producers were found the forest.

Seventy three ant species were directly observed in trophobiotic interaction with hemipteran. Some of these species were also found among EFN and FN visitors (Annex 1). Fifteen ant species presented three or more interactions with 17 hemipterans (Table 3).

Table 3. Distribution of *Stictococcus vayssierei* host plants recorded in the different vegetation type. The number of infested plants is presented in brackets

Family	Plants species	Fallow	Forest	Mixed	Total
Zingiberaceae	*Aframomum daniellii* K.Schum.	6	37	0	43 (4)
Fabaceae	*Arachis hypogaea* L.	0	0	57	57(31)
Araceae	*Colocasia esculenta* (L.) Schott	2	0	0	2 (1)
Costaceae	*Costus afer* Ker Gawl.	52	15	0	67 (1)
Dioscoreaceae	*Dioscorea sp*	1	2	0	3 (0)
Marantaceae	*Haumania danckelmaniana* (J.Braun & K.Schum.) Milne-Redh.	18	57	3	78 (0)
Euphorbiaceae	*Manihot esculenta* Crantz	30	0	165	195 (124)
Commelinaceae	*Palisota hirsuta* K.Schum.	1	8	0	9 (0)
Araceae	*Xanthosoma mafafa* Schott.	3	0	52	55(21)
	Total	113 (34)	119 (2)	277 (146)	509 (182)

Association between ant and hemipteran (Table 4) was different from random in the three vegetation types and was highly significant in the mixed-crop field: fallow ($H'_2 = 0.36 \pm 0.11$); forest ($H'_2 = 0.19 \pm 0.07$); mixed-crop field ($H'_2 = 0.92 \pm 0.07$). The main interaction in the mixed-crop field was observed between *S. vayssierei* and *A. tenella.* At the species level, specialization index was high for *A. tenella* (0.86 ± 0.06) and also *S. vayssierei* (0.97 ± 0.02). The abundance of *S. vayssierei* host plants was higher in the mixed-crop field than in the fallow and forest (Table 3). Association between ant and plants hosting hemipteran was different from random in the three vegetation type, mainly in the mixed-crop field: fallow ($H'_2 = 0.29 \pm 0.01$); forest ($H'_2 = 0.20 \pm 0.05$); mixed-crop field ($H'_2 = 0.77 \pm 0.03$).

Table 4: Association between honeydew-producing insects, ants, and host plants of trophobionts. Numbers are interaction frequencies on different plant individuals. Only species presenting more than two cases of interactions with hemipteran are represented. For full ant names, see Annex 2.

Hemipteran	Ant species	Fallow	Forest	Mixed	Total
Aphididae	*Camponotus flavomarginatus*	3	0	5	8
	Crematogaster striatula	8	0	1	9
	Monomorium bicolor	0	0	4	4
	Myrmicaria opaciventris	0	0	9	9
	Camponotus acvapimensis	6	0	0	6
	Camponotusmaculatus	2	0	1	3
Pseudococcidae	*Crematogaster striatula*	15	10	1	26
	Technomyrmex lujae	2	4	0	6
	Camponotus acvapimensis	5	1	0	6
	Crematogaster inconspicua	3	0	1	4
	Myrmicaria opaciventris	3	0	2	5
	Tetramorium aculeatum	5	0	0	5
Coccidae	*Crematogaster striatula*	6	27	1	34
	Crematogaster zavattarii	0	5	0	5
	Crematogaster costeboriensis	0	3	0	3
	Oecophylla longinoda	0	3	0	3
	Technomyrmex lujae	0	44	0	44
	Tetramorium aculeatum	3	0	0	3
	Oecophylla longinoda	5	5	0	10
	Technomyrmex kohli	0	3	0	3
Stictococcidae	*Anoplolepis tenella*	32	2	136	170
(*Stictococcus vayssierei*)	*Pyramica maynei*	0	0	5	5
Total		98	107	166	371

Co-occurrence

One hundred and thirty six cases of co-occurrence between two or more ant species were recorded. Co-occurrence was more common on nectar (64.7%, n = 136) than on honeydew sources (35.3%, n = 136) (Table 5).

Table 5: Percentage of co-occurrence of ant species foraging on extrafloral nectaries (EFNs), floral nectaries (FNs), or honeydew sources (per plant individual). N= number of records per plant during all survey. Different letters in the χ^2 column indicate significant differences between resources in frequency of ant co-occurrence (χ^2 test based on absolute frequency between all three pair wise resource combinations)

Resources	N	1sp.	2sp	3sp	>3sp	χ^2
EFNs	391	79.8	12.3	5.1	2.8	a
FNs	68	72.1	19.1	5.9	2.9	a
Honeydew	495	90.3	6.7	2.4	0.6	b

Ants co-occurred on 36 plant species in all surveys with 14 plants having at least five observations. Greatest occurrence was recorded on *Alchornea cordifolia* (17.6%, n = 136). *Crematogaster striatula* and *Myrmicaria opaciventris* were species that co-occurred most with other species (11.0% and 9.5% respectively, n = 136) (Figure 2).
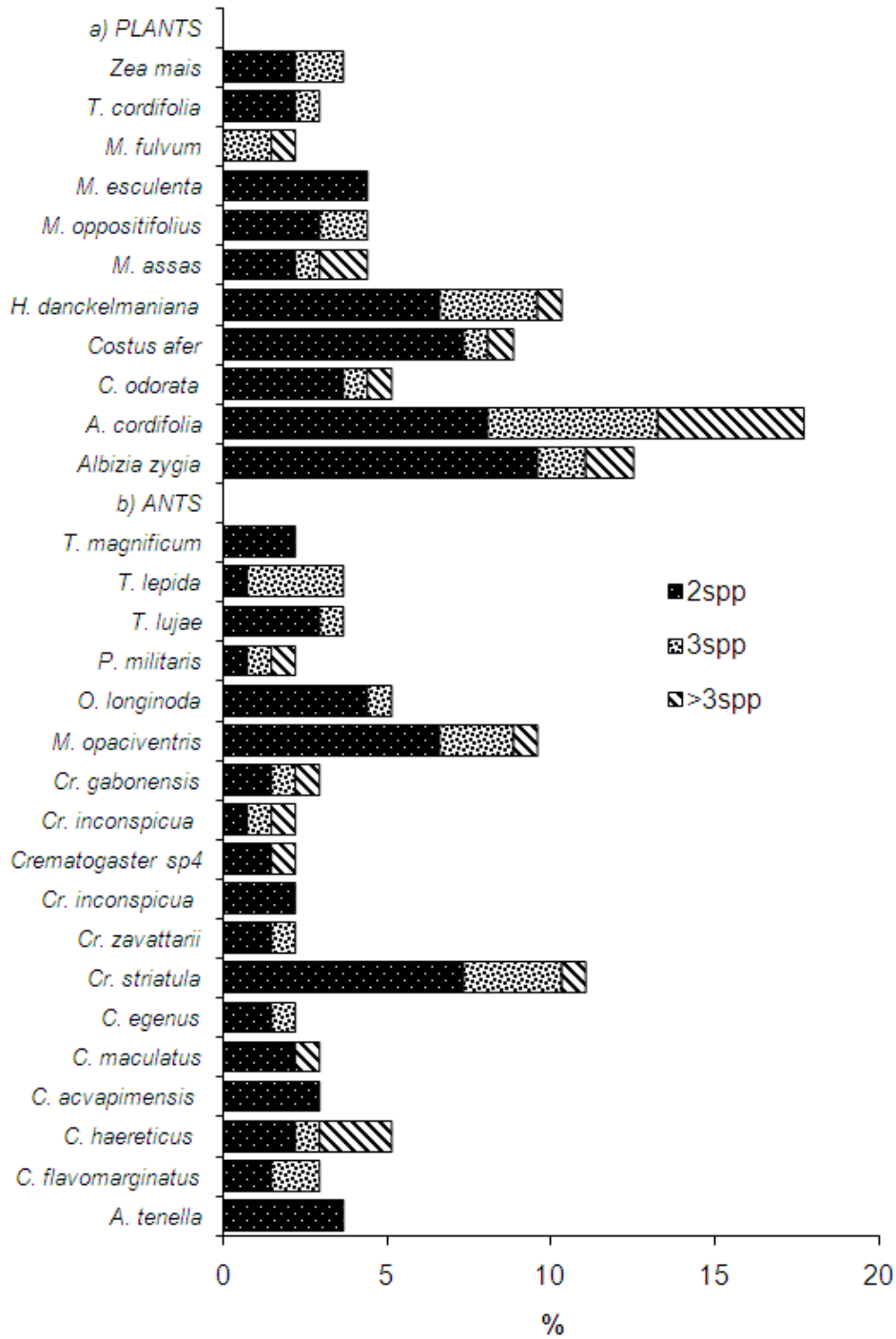
Fig. 2 Frequency of co-occurrence of two, three or more ant species on the same plant (a) by ant species and (b) by plant species with extrafloral (EFN) or floral nectaries (FN). Only surveys with a minimum of three observations were considered

DISCUSSION

Results from this study suggest that nectar and honeydew are important factors that shape distribution patterns in an ant assemblage in the humid forest zone of southern Cameroon. Extrafloral nectar is regarded as a general ant reward, capable of attracting to the plant a wide diversity of ants (Di Giusto et al. 2001; Janzen 1966). Many ant species visited EFN-producing plants and some hypotheses of the structuring mechanisms of the ant assemblage in our study area could be deducted:

Resource quality and quantity

Food quality and quantity may play an important role in the partitioning of ant species attendance. Honeydew consists of amino acids (Douglas 1993; Völkl et al. 1999) and a large spectrum of carbohydrates dominated by the trisaccharide melezitoze (Fischer et al. 2005; Hogervorst et al. 2007). Nectaries are often more limited regarding its sugar (sucrose, fructose and glucose) and amino acid content. If nectar is less nutritive than honeydew, monopolization should be less economical. However, nectar composition varies greatly between plants species and it has been demonstrated that nectar composition from *Flagella* and *Smilax* is similar to honeydew (especially in amino acid content) and EFN of these two plants are monopolized by dominant ants (Bluethgen and Fiedler 2004; Bluethgen et al. 2004).

Nectar sources were visited by a large spectrum of ant species as reported in many other studies, including opportunistic species. Although EFNs attract a variety of nectar-feeding insects, ants are by far the most frequent visitors to EFN-bearing plants both in temperate and tropical habitats (Koptur 2005; Oliveira and Brandão 1991). We noticed that some ant species overlapped in their choices of plant species visited for nectar, leading to low specialization index ($0.14 < H_2' < 0.28$). This pattern has been recorded in many other studies and results are summarized in Blüghten et al. (2007). Our results showed considerable variation among habitats in the number, diversity, and spatio-temporal distribution of ant assemblage which could be explained by the inter-habitat differences of distribution patterns of EFNs plants. Therefore, the diversity of the vegetation can be considered as a structuring factor of the ant assemblage (Rico-Gray et al. 1998).

Ant assemblage present at honeydew sources was different from that observed on nectar, and co-occurrence of ants on hemipteran species was less frequent. Hemipteran trophobionts are third partners in a large proportion of ant myrmecophyte mutualisms and their importance appears to vary among systems (Davidson and McKey 1993). Many ant species commonly tend hemipteran (mostly aphids, membracids and scales) and feed on their energy-rich honeydew. In the course of ant tending, hemipteran insects frequently receive a wide range of beneficial services, including protection from predators and parasitoids (Buckley 1987; Cushman and Addicott 1991; Way 1963). The partitioning of honeydew producers among ant species was pronounced. This could be explained by the fact that many honeydew-collecting ant species either maintained high worker density on the plant foliage (Fig. 3A) or built shelter to cover entirely the trophobionts colony so that other ant species could not access the honeydew source (Fig. 3B).

Fig. 3 Honeydew monopolization by *Technomyrmex lujae* through high worker density (A) and by *Crematogaster striatula* through the construction of a shelter (here partially opened) (B)

Although hemipteran can be regarded as major pests to many plant species, ant-tended hemipterans may indirectly benefit their plant hosts through protection against external herbivores whose damage to the plant outweighs the cost of hemipteran infestation (Buckley 1987; Messina 1981). Since ant communities are strongly hierarchical, competitively dominant and territorial species can be distinguished from competitively inferior species and the distribution of the latter may be partly controlled by the dominant species (Bluethgen et al. 2000; Savolainen and Vepsäläinen 1998).

Hierarchy among ant species

Dominant ants often monopolize some nectaries and hemipteran aggregations, whereas subordinate ants are more opportunistic and commonly share nectaries with other species simultaneously (Bluethgen et al. 2000). Trophobiont monopolization in our study was observed with *Oecophylla longinoda* (associated with *Stictococcus sjostetdi* on *Costus afer*), *Crematogaster striatula* (associated with *Stictococcus sjostetdi* on several plants), *Technomyrmex lujae* (associated with *Stictococcus sjostetdi* on *Myrianthus arboreus*), *Anoplolepis tenella* (associated with *Stictococcus vayssierei* on *Manihot esculenta* and *Xanthosoma mafafa*). The association between *Anoplolepis tenella* and *S. vayssierei* differs from the other associations on two points: its location and its specialization. (a) *A. tenella* tends *S. vayssierei* colonies on the underground part of the plant where it builds its nest. Because of this hidden location, other ant species may not have access to the honeydew source. (b) *S. vayssierei* was consistently tended by *A. tenella* thus justifying the high specialization index at both species levels. This association has been already reported elsewhere (Dejean and Matile-Ferrero 1996; Fotso Kuate et al. 2006, 2008; Tindo et al. 2009), and may have contributed to the highest level of specialization between hemipteran and ants in the mixed-crop field. This association appears to be obligatory for the scale on two points: Firstly, considering the scale anatomy and physiology, the anal orifice is situated in the middle of the dorsum and the scale doesn't possess (or have lost) the ability to eject the honeydew away from the body as some soft scale insects do (Tindo et al. 2006; Ben-Dov and Hodgson 1997; Williams et al. 2010); Secondly, the scale adult stage is sedentary and the dissemination is done by *A. tenella* workers through the crawlers which are the mobile stage (Fotso Kuate et al. in prep.). The combination of these factors renders the scale vulnerable to pathogens which will develop of the honeydew if left uncollected.

Whether through numeric dominance or shelter, honeydew monopolization is a factor that limits competition within the ant assemblage and reduces co-occurrence the source. Ant-hemipteran associations are well known to be for mutual benefit (Buckley and Gullan 1991; Del-Claro and Oliveira 2000) although some studies had not confirmed this view (Zachariades et al. 2009). The potential benefit to the plant, which can be protected by the predatory behavior of the ant against herbivores is not always clear and can be controversial (Mody and Linsenmair 2004; Ness and Bronstein 2004). The presence of the ant-hemipteran association can be beneficial to the host plant only if hemipteran populations are low and they are not vectors of plant diseases.

But in many cases, the association leads to the proliferation of the hemipteran insect and consequently increasing damage host plant (Dejean and Matile-Ferrero 1996).

Generally, ants that attend hemipteran are not specific and several ant species can simultaneously visit such as cicadellid, delphacid or membracid species (Larsen et al. 2001). This was observed in our study as the majority of co-occurrence at honeydew source was observed with aphids and membracids. Many others factors may inhibit or facilitate coexistence or simultaneous exploitation of a resource by different ant species: (a) The architecture of the plant: honeydew sources were often concentrated on certain plant parts and sometimes hidden in domatia at the opposite of many nectar that are scattered over the foliage, thus allowing simultaneous visitation of the plant by many ant species; (b) The benefit to the ants: Benefits from resource monopolization should increase with the predictability of a source. Honeydew is certainly one of the most predictable and stable resources. It can be largely controlled by the ants themselves and it is less subjected to scarcity than other available resources (McKey and Meunier 1996). However, honeydew of some hemipteran species can be very variable in its nutritional suitability for honeydew consumers and can be far inferior to nectar and sucrose (Wäckers 2000; Wäckers et al. 2007).

In conclusion, inter-habitat differences in the distribution of EFN-producing plants, hemipteran and spatio-temporal pattern can be considered important as structuring mechanism of the ant assemblage in southern Cameroon.

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Chapter 4: Transport and dispersal of *Stictococcus vayssierei* (Homoptera, Stictococcidae) by *Anoplolepis tenella* (Hymenoptera, Formicidae)

Running head: Dispersal of *S. vayssierei* by *A. tenella*

Suggested Journal: Journal of Insect Behaviour

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Abstract

We conducted a series of experiments and observations with the aim of determining the dispersal mode of the African root and tuber scale *Stictococcus vayssierei*, a pest on cassava. We monitored the main options of dispersal that occurred in scale insects: wandering of crawlers, active dispersal by ant workers, phoresis on colony-founding queen ants and passive dispersal by wind. Results showed that *A. tenella* workers are actively involved in the transport and dissemination of scale crawlers. When ants were excluded, crawlers could move by themselves for short distance to find the host plant. In the presence of ants, crawlers were transported by workers and established on initially clean cassava cuttings. Scales transport was affected by time and ant density. Neither a case of phoresis nor dispersal by air currents was recorded, suggesting that passive dispersal is rare. These results outline the active role of *A. tenella* workers in the dispersal of immature stages of *S. vayssierei* in Southern Cameroon.

Key words: *Anoplolepis tenella*, *Stictococcus vayssierei*, active dispersal, wind dispersal; phoresis

Introduction

Dispersal can be a crucial factor affecting fitness in insects (Kindlmann et al. 2007). In Coccoidae, the dissemination of individuals is mainly observed in the highly mobile first-instar nymphs (crawlers), which have relatively well developed antennae and legs (Beardsley and Gonzalez 1975; Gullan and Kosztarab 1997; Williams 1997). Two main modes of dispersal can be outlined: passive dispersal through phoresis (i.e., sitting on some other moving organism) or by air currents, and the wandering of crawlers which is thought to serve for short range movement. The long-distance dispersal of many species of Coccoidae is also related to human activities through the exchange of planting materials or through phoresis on human clothes or animal hair (Simmonds and Greathead 1977; Washburn and Frankie 1981; Washbum and Washburn 1984). Many studies have also demonstrated the importance of wind in the dispersal

of coccids crawlers (Quayle 1916; Greathead 1972; Washbum and Washburn 1984; Greathead 1997).

Wind dispersal and wandering of crawlers are not the only dispersal options available to scale insects. Mutualistic ants often engage in active or passive dispersal of the tended hemipteran (Way 1963). Many factors can induce the transport of the trophobionts by the tending ant including nest disturbance, nest movement and new feeding sites as observed in *Pseudolasius* spp. associated to roots mealybugs *Planococcoides* sp. and *Maconellicoccus multipori* (Malsch et al. 2001). Workers of *Oecophylla longinoda* were observed transporting *Saissetia zanzibarensis* and establishing them at suitable feeding sites (Way 1954).

Earlier studies outlined the transport of coccids to uninfested host plants by ants of the genus *Crematogaster* (Das 1959) and *Oecophylla* (Way 1954). Several authors have indicated that ants may carry crawlers in their mandibles to suitable feeding sites or to different host plants, thus assuring their dissemination (Beardsley and Gonzalez 1975; Washburn and Frankie 1981; Gullan and Kosztarab 1997; Johnson et al. 2001). However, experiments with *Solenopsis geminata* and *Brachymyrmex heeri* Forel could not provide evidence of any role in the dissemination of their trophobiont *Saissetia coffeae* (Smith 1942). This was also the case between *Anoplolepis custodiens* (F. Smith) and its trophobionts *Coccus hesperidum* (Steyn 1954).

Other myrmecophilous Coccidae are carried by colony-founding queen ants (Buschinger et al. 1987; Klein et al. 1992; Gaume et al. 2000). During their nuptial flight, young females of the genus *Acropyga* transport root mealybug for subsequent colony foundation (Johnson et al. 2001). The queen carries the crawlers, which they introduced onto host plants to develop and then provide the initial food source (i.e., sugary secretion) for the developing brood. This type of queen-assisted dispersal is likely to be very important in long-distance dispersal of the trophobionts. It is very important to know if such a phenomenon occurs with *Anoplolepis tenella* Santschi particularly for understanding the diversity and dispersal of *S. vayssierei* populations. This subterranean scale is found in area of over 2 million squares kilometers (Hanna et al. personal observations) and might very well depend on its tending ant for short and long-range dispersal. While we strongly suspected that *Stictococcus vayssierei* are dispersed by *Anoplolepis tenella*, there was so far no experimental evidence of *A. tenella* role in the dispersal of the scale, except for anecdotal observations of *A. tenella* workers with scale crawlers in their mandibles.

We conducted a series of experiments to determine if *A. tenella* indeed actively engages in dispersal of *S. vayssierei*, and investigated a few of the possible factors that may affect the extent of such behaviour.

Material and methods

The experiments were conducted in the screenhouse at the International Institute of Tropical Agriculture (IITA) station in Yaoundé, Cameroon, from November 2007 to October 2008 (average temperature ± SD: 23.63 ± 3.73 °C; average humidity ± SD: 84.04 ± 16.00 %; n= 1680 measures). The experiment consisted of longitudinal half-barrel sections (90cm x 60cm) and 20 L-plastic basins filled with top soil (i.e., 20 cm in depth). Four 30 cm leg supports were added to elevate the barrels. Soil was collected from non-infested cassava field near the IITA Campus at Nkolbisson (N 03° 51.850'; E 011° 27.767'; 759 m. Results of the chemical analysis performed at the Soil Chemistry Laboratory of IITA are displayed in Table 1. Barrels and basins were positioned on a metallic table and watered twice a week, thus allowing the sprouting of cassava cuttings. Average soil temperature in the barrels and basins at 13 cm from the surface was estimated 24.27 ± 2.08 °C, n = 480 measures). Cassava cuttings (variety 98/0506) were obtained from IITA nursery plots managed by the breeding unit.

Table 1: Characteristics of top soil used in barrels and basins during the experiment

	pH	Ca	Mg	K	P	Total N	Organic C
Value	4.81	3.29	1.82	0.23	3.59	0.14	1.55
Indication	Water	cmol(+)/Kg = me/g			ppm	%	%

Ca=Calcium; Mg=Magnesium; K=Potassium; P=Phosphor, N= Nitrogen; C= Carbon

Crawler movement

Cassava cuttings (10 cm in length) were planted in seven rows spaced by 11cm along the barrels' length. Adult *S. vayssierei* females collected from infested cassava field at Atin-odzoe (03°

48'08''N; 11° 22'42''E; 809 m a.s.l.) were incubated in Eppendorf tubes to produce crawlers for use in the experiments. This technique allowed us to obtain more than two thousand crawlers from 570 incubated scale females.

Two weeks after the sprouting of cassava cuttings (plant average height: 5.17 ± 0.14 cm, n = 100), 50 crawlers were released either at the edge of the barrels (10 replicates) or at its center (10 replicates). We monitored crawlers' movement after their release for five minutes. Cutting infestations with crawlers at various distances from the release point was determined three days after their release. The experiment was repeated with each barrel hosting a pre-established ant colony (5 queens + 500 workers) collected from cassava fields with their nesting materials.

Crawler dispersal by ant workers

The basic set-up consisted of 20-litre plastic basins filled with top soil from a mixed-crop field where *S. vayssierei* was absent. Three non-infested cassava cuttings were planted in each basin. Fragments of *A. tenella* colonies and infested cassava storage roots were collected from a scale infested cassava field in Atin-odzoe. The number of ants from each fragment was estimated and they were introduced into the basins after sprouting of the cassava cuttings. Two ant densities levels were considered: high density (3 queens and ca. 700 workers per barrel) and low density (1 queen and ca. 300 workers per barrel). We also considered two scale densities levels: high density (264.4 ± 34.5 adults per barrel) and low density (81.8 ± 12.1 adults per barrel). Five replicates were set for each combination of ant and scale density levels. Cassava cuttings infested with scales were deposited at the surface of the basins to produce crawlers. During the course of the experiment, 7617 adult females were placed on the surface of the basins, but the number of crawlers they produced could not be evaluated. This technique was used because crawlers produced in Eppendorf tubes might be weak since the adult females do not feed during the incubation period.

Each infested basins (basins with ants and scales) was then connected by a bridge to a similar basin containing three cassava plants without ants and scale (non infested basin). Bridge was made up with transparent plastic tube (Ø: 15 mm; length: 30 cm). The centre of each bridge had a gap wide enough to prevent scale crawlers from crossing from infested basin to non infested basin, while allowing the passage of ant workers (Way 1954). Control basins were not

connected to infested basins. The borders of each basin were lined with petroleum jelly to prevent the ants from moving from one basin to another by any other means except through the bridge. We monitored ant activity at the surface of the two connected basin and on the bridge during 15-min observations twice a week and during known periods of *A. tenella* surface activity (Fotso Kuate *et al.*, 2008). Ants carrying scale crawlers were noted. One month after the introduction of ants and scales into the basins, half of the experiments set up was evaluated and the scale presence on cassava cuttings were recorded on initially clean cassava cuttings. The rest of the experiments were evaluated two months after.

Crawler dispersal by wind

Double-sided sticky yellow cards (126 mm x 77 mm) were hanged at 1.5 m above the ground level in cassava fields from November 2007 to February 2009. Five cards were set per field with sides facing opposite directions. A total of 30 cards were installed in fields and they were replaced at two-week interval. All the cards collected in the fields were wrapped in a transparent plastic paper and observed in the laboratory under a stereomicroscope.

Crawler's dispersal by phoresis on *A. tenella* queens

In addition to dispersal of scale by *A. tenella* workers, which probably occurs over relatively short distances, we determined the possibility of scale dispersal by alate queens during nuptial flights, which are mostly observed in September in southern Cameroon (Fotso Kuate *et al.*, unpublished data). Alate queens was collected after nuptial flight from strategically placed light traps in the fields and inspected for the presence of *S. vayssierei* crawlers.

Statistical analysis

Factors susceptible of affecting scale dispersal were taken into account during the analysis: the scale density, the ant density, the time and the initial basin status (infested or non-infested). For scale and ant density, experiments considered the two factors simultaneously and consisting of two levels – low and high - of each factor following the same experimental set-up as described

above. We used the General Linear Model to investigate the effect of above mentioned factors on the number of scale counted on previously clean cassava cuttings. Analysis was done with SAS software version 9.2 (SAS 2008).

Results

Crawler movement

In the absence of *A. tenella* workers*,* 21 crawlers out of ca. a thousand individuals (2.1 %) survived in twelve barrels (out of 20). These individuals were recorded on cuttings located at 11 cm from the release point. When the cuttings of the first rows were removed in five barrels, a single individual was recorded on the cuttings of the second row (22 cm) after three days. When the experiment was repeated in the presence of ants, *A. tenella* workers were observed carrying crawlers after the release (n = 122 observations) (Fig. 1). Three days thereafter, we recorded 201 crawlers (20.1 %) on cuttings in twenty barrels. Distance from the release point varied from 11 cm (157 individuals on first row of cuttings) to 55 cm (eight individuals on fifth row of cuttings).

Fig. 1 *Anoplolepis tenella* worker transporting *Stictococcus vayssierei* crawler.

Dispersal of crawlers by *A. tenella* workers

One month after the beginning of the experiment, *S. vayssierei* crawlers and a few young adults were found on the formerly clean cassava cuttings in the infested basins (2.59 ± 0.49 scales) and

non-infested basins (1.45 ± 0.49 scales). The average number scale recorded on initially clean cassava at one month was 2.02 ± 0.57 scales (Table 2).

After two months, the number of scales that were counted on cassava cuttings in the non infested basins (5.15 ± 0.87 scales) was slightly lower than the one counted in the infested basins (5.98 ± 0.87 scales). The average number scales recorded on cassava after two months was 5.56 ± 0.57 scales, which was significantly higher than the number recorded at one month ($F_{(1,74)}$ = 21.04; $p < 0.0001$) (Table 2). Non-infested basins which were isolated from the infested basins remained free from scale infestation until the end of the experiments.

Effect of ant and scale density on the dispersal of crawlers

The total number of scales that infested the newly planted cassava cutting was affected by the ant density ($F_{(1,74)}$ = 8.37; $p = 0.005$). With high ant density, the number of scales (4.64 ± 0.94 scales) that was transported across the bridge to the non-infested basin was higher than the number recorded with low ant density (2.08 ± 0.89 scales). The same trend was observed in the infested basin with high ant density (5.24 ± 0.64 scales) compared to that observed with low ant density (3.43 ± 0.61 scales). Overall, infestation of cassava cuttings with high ant density (4.94 ± 0.53 scales) was significantly higher than that recorded with low ant density (2.76 ± 0.56 scales) (Table 2).

Unlike for ants, scale density did not significantly affect infestation of newly planted cassava cuttings ($F_{(1,74)}$ = 1.81; $p = 0.183$). With initial high scale density, the number of scales that was transported across the bridge to the non infested basin (3.88 ± 0.94 scales) was slightly higher than the number recorded when the experiment started with low scale density (2.77 ± 0.89 scales). The same trend was observed in the infested basin with high scale density (4.67 ± 0.64 scales) compared to low scale density (3.95 ± 0.61 scales). Overall infestation of new cassava cuttings was higher (4.27 ± 0.56 scales) with high scale density compared with low scale density (3.36 ± 0.53), although the difference was not significant (Table 2).

Table 2 Average number of scale individuals (all developmental stages pooled) on previously clean cassava cuttings in infested and non-infested basins. The comparison used GLM to analyses the effect of ant and scale density on the number of scale individuals counted on initially clean cassava cuttings of *S. vayssierei* crawler dispersal.

Variables	Infested basin	Non Infested basin	Pooled	Comparison
One month	2.59±0.49	1.45±0.49	2.02±0.57	$F_{(1,74)}$=21.04; p<0.0001
Two months	5.98±0.87	5.15±0.87	5.56±0.57	
Low ant density	3.43±0.61	2.08±0.89	2.76±0.56	$F_{(1,74)}$=8.37; p=0.005
High ant density	5.24±0.64	4.64±0.94	4.94±0.53	
Low scale density	3.95±0.61	2.77±0.89	3.36±0.53	$F_{(1,74)}$=1.81; p=0.183
High scale density	4.67±0.64	3.88±0.94	4.27±0.56	

Note: Non infested basin initially had clean cassava plants and was then connected to infested basin also with clean cassava plant but with added scale-infested cassava at the surface.

Dispersal of the scale by alate *A. tenella* queens and by air currents

On six occasions, 1243 queens were collected after nuptial flight from light traps. Close inspection showed that none of them was carrying scale crawlers between mandibles or anywhere else on the body. Also, no crawler was recorded on sticky traps during the three months period of observation in the field, suggesting that wind-dispersal of *S. vayssierei* crawlers is absent or rare.

Discussion

Our study provides evidence that *S. vayssierei* crawlers are transported from one plant to another by *A. tenella* workers. Scale infestation occurred on formerly clean cassava cuttings in the non-infested basins, despite the gap on the bridge. This gap (see methods) did not allow dispersal of the mobile stages of *S. vayssierei* unless transported by *A. tenella* workers. This phenomenon

was earlier observed with workers of *O. longinoda* carrying young stages of the coccid *Saissetia zanzibarensis*. The ants established them on young twigs and solicited honeydew through antennal palpation for a few seconds before departing (Way 1954).

Transport can be one of the benefits derived by hemipteran from association with ants along with protection from natural enemies and subsequent increase in colony growth (Way 1963), although many ant species do not engage in transporting their homopteran trophobionts (Way 1954). However, the transport of hemipteran by attendant workers of certain species of *Lasius, Acropyga,* and *Oecophylla* is well substantiated (Johnson et al. 2001).

For some species like *Lasius niger*, the behavior of the workers towards their associated hemipteran is identical with their behavior towards their brood and a virtually unmodified brood care instinct determines transport and nursing behavior of these ants towards attended aphids (Pontin 1960).

In our experiments, transport was affected by ant density. With low ant density and high scale density, honeydew was left uncollected and newly emerged crawlers sank into it. The presence of more ants significantly increased the transport of crawlers across the bridge and the infestation of new cassava cuttings. This could be interpreted in two different ways which are not exclusive. First, we can consider that the presence of more ants increased the probability of finding mobile crawlers and locating a cutting in both infested and non infested basins. Secondly, if we consider that honeydew produced by *S. vayssierei* is an important component in the diet of *A. tenella* (Fotso Kuate et al. 2008), the presence of more workers increases the demand of food supply for the colony. Therefore *A. tenella* could increase its chances of getting food for the colony by putting more crawlers on cuttings to produce honeydew. This last hypothesis is likely to occur in the fields as increasing scale density on cassava plant is usually correlated with an increasing ant density under those plants (Fotso Kuate 2003).

Dispersal via air currents is also a mechanism by which some scale insects, mainly armored scales, are dispersed between host plants within an area (Greathead 1989). This method of dispersal cannot however explain long range dispersal which sometime extends to several kilometers. *Stictococcus vayssierei* living and feeding on plants roots and tubers do not seem to use this mode of dispersal as indicated by their absence on sticky traps.

Many trophobionts are known to be dispersed by ant queens during colony fission or foundation. Young females of *Tetraponera* sp. which lives within the large hollow internodes of

giant bamboo transport their trophobionts to empty bamboo internodes that had been previously excavated by stem-feeding pyralid caterpillars (Johnson et al. 2001). Co-dispersal of the plant ant *Aphomyrmex afer* and its coccids are done through phoresis (Gaume et al. 2000). Such behavior has not been observed in *A. tenella - S. vayssierei* system, strengthening the idea of dispersal by workers.

Scale dispersal is unlikely to occur during the dry season. Survey on scale population dynamic and cassava screening experiments showed that during the dry season, scale density on host plants decreased drastically with higher mortality level in adults and less crawler emergence (R. Hanna, unpublished data). Scale populations rebound after the rainy season, thus suggesting the possible effect of season on the dispersal of *S. vayssierei* in southern Cameroon.

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Chapter 5: Toxicity of Amdro, Borax and Boric Acid to *Anoplolepis tenella* Santschi (Hymenoptera: Formicidae)

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Abstract

Anoplolepis tenella Santschi (Hymenoptera: Formicidae) is associated with the proliferation of the cassava pest *Stictococcus vayssierei* Richard (Hemiptera: Stictococcidae) in central Africa. Amdro, Borax and Boric acid solution were evaluated in the laboratory for toxicity against *A. tenella* colonies. Workers were exposed to bait for ten days during primary screening and colonies for six weeks during secondary screening. Mortality was recorded daily for each toxicant. The results indicated that each of the three toxicants displayed delayed toxicity with less than 15% mortality after the first day. In comparison to Amdro and Borax, 1% Boric acid was more effective in killing ant workers. Boric acid-sucrose solution reduced the numbers of workers and brood by 90% within 6 weeks. Experiments under semi-field condition in a screenhouse indicated that significant reduction of *A. tenella* densities can be achieved under natural conditions when using Boric acid-sucrose bait.

Key words: *Anoplolepis tenella*, cassava, lethal time, pest, *Stictococcus vayssierei*, toxic bait

Introduction

Insecticide spray had been used to control pest ants often as a barrier treatment (Klotz et al. 2002; Klotz et al. 2003; Rust et al. 2004). Although this method showed some significant results, it also has limits as only foraging ant workers are affected. These foragers represent only a small entity of the colony population. Queens which assure the colony reproduction are not affected, and in these conditions, long term control cannot be expected (Knight and Rust 1990; Rust et al. 1996). Therefore, developing a strategy which permits to tackle all members of the colony for a sustainable control is of high importance.

Toxic baits are ideal for the effective control of pest ants because they transport the toxicant back to the nest and share it with other members of the colony. This replaces the difficult and laborious task of finding and treating a nest site that may be located in an inaccessible area (Tripp et al. 2000). The advantages of toxic baits include, among others, (a) their ease of use; (b) that their efficacy is not affected by soil type; (c) that one or two treatments are sufficient for long-term control, (d) that the toxicant is spread to all members of the colony (therefore colony movement is not a problem); (e) that toxic baits can be target specific and may only be taken up by species that have common food preferences; and 6) that treatment requires a very small amount of toxicant compared with insecticidal spray, thus reducing contamination of the environment (Davis and van Schagen 1993; Collins and Callcott 1998).

There are different toxicants, or active ingredients that are used in commercially available bait products, specifically registered for use against ants. Some active ingredients interfere with reproduction and are often referred to as insect growth regulators. Amdro, Borax and Boric acid were chosen for the experiment based on their availability and references from previous experiments on ant control (William 1983; Klotz et al. 1996; Klotz et al. 2000a; Klotz et al. 2000b; Daane et al. 2006).

Amdro is a slow-acting metabolic inhibitor that kills all members of a colony that ingest it. It was first formulated in soybean oil-defatted corn grit baits and registered in the USA as Amdro in 1980 for control of the red imported fire ant *Solenopsis invicta* (Williams et al. 2001). Amdro has been used effectively against many other ant species, e.g., *Pheidole megacephala* (Hoffmann and O'Connor 2004)*, Monomorium destructor,* and *Wasmannia auropunctata* (Causton et al. 2005). It is considered to be a minimum risk to non-targets because of its low

102

toxicity to vertebrates and also because it cannot be absorbed through the insect cuticle and do not accumulate in the environment (Vander Meer et al. 1982; Bacey 2000).

Borax is a natural mineral compound which acts as a stomach poison. As an insecticide, Borax can be used in a toxic bait formulation or as a dry powder. The insects ingest the powder from eating or from cleaning their legs after walking in the powder. Upon accumulating the sodium borate in their system the insect's metabolism and reproductive system is inhibited and they die (Ebeling 1995).

Boric acid bait has been widely used for the control of different pest ant species such as the Argentine ants and the imported Red Fire Ant (William 1983). It is a slow acting inorganic insecticide and its main quality is the high solubility in water, into which attractants such as foods odors, pheromones and sugars can be added (Ebeling 1995; Klotz and Moss 1996; Klotz et al. 1996; Klotz et al. 1997a; Klotz et al. 1997b; Klotz et al. 1998).

Anoplolepis tenella is a tropical ant species commonly associated to the African root and tuber scale *Stictococcus vayssierei,* a pest that infests at least ten cultivated crops with greatest occurrence on cassava (Dejean and Matile-Ferrero 1996; Ambe et al. 1999; Ngeve 2003; Tata-Hangy et al. 2006). Several indigenous plants also serve as reservoir for the scale in fallows and forest from which they moved onto the crop during cropping season (Tindo et al. 2009). It has been demonstrated that the ant workers transport scale crawlers from infested cassava plant to newly planted cassava cuttings (Fotso Kuate et al. in prep). Therefore, plans to develop control option against the scale in central Africa are contingent to the reduction of the density of the associated ant in cassava fields. This study aimed to evaluate the effect of Amdro, Borax and Boric acid on *A. tenella* colonies collected in the field and maintained under laboratory conditions.

Materials and methods

Colonies of *A. tenella* used in this study were collected from cassava fields and fallows at the village of Atin-odzoe (03°48'08"N; 11°22'42"E; 809 m a.s.l.) in the Center region of Cameroon. After nest excavation, queens, workers and brood were collected with nesting material, put in paper bags and brought back to the laboratory. Individuals were then removed from the soil using a mouth-aspirator, counted and introduced into artificial nests which

consisted of glass tubes of 15 cm in length and 2 cm diameter filled to the third of its capacity with distilled water. A 3-cm thick piece of cotton wool was then jammed up to the level of the water. The remaining space in the tube served as ant rearing chamber. Each tube was wrapped with aluminum foil and fixed at the bottom of a plastic box (25 cm x 10 cm x 10 cm) which served as the foraging arena. Soya oil was applied to the edges of these boxes to prevent the ants from escaping.

Colonies were fed at two days interval on a standardized laboratory liquid diet, a mix of 900 ml 10% sucrose solution and 100 ml of honey. A supplement of laboratory-reared grasshoppers was cut into small pieces and offered as protein source. Grasshoppers were reared in cages in the screen house and fed with millet leaves. A bucket with sand was placed in their cages for the female to lay eggs. Immature stages were collected after they had emerged from the sand and kept frozen in the laboratory. All colonies were set in the rearing chamber for one month prior to the experiment (average temperature $\pm$ SD: $24.7 \pm 1.3\,^{\circ}$C; average humidity: 69.4 $\pm$ 3.9 %).

Isolated workers and colonies were then exposed to Amdro (Fisher Scientific, UK), Borax (99.1% acidimetric; CAS n$^{\circ}$ 1330-43-4, Fisher Scientific, UK), and Boric acid (99.8% acidimetric, CAS n$^{\circ}$10043-35-3, Fisher Scientific, UK). Amdro was used in its granular formulation and Borax as powder. Dry powder of Borax and other boron material can act as stomach poison and are abrasive to the insects' exoskeleton. Both destruction of the digestive tract and penetration through the cuticle contribute to insect mortality (Ebeling 1995; Wang and Bennett 2010). Boric acid was dissolved in water to obtain concentrations 0.1, 0.5 and 1%. Screening methods were adapted from literature (William and Lofgren 1981; William 1983).

Primary screening

During primary screening, twenty ant workers from laboratory colonies were starved for 3 days and then placed in 1L disposable plastic boxes 24 hrs preceding the test. This pretreatment holding period allowed the ants to adjust to the experimental condition prior to the start of treatments. Boric acid solution was filled in 1.5 ml-plastic vials with a cotton wool as a stopper. One gram of Amdro and Borax were offered in a Petri dish and placed in the plastic box containing the ants in the respective treatments. Workers were allowed to feed solely on it for 48 hrs. Thereafter, new Petri dishes containing cotton soaked with laboratory liquid diet were placed

in the boxes and replaced at two day-interval for the remainder of the test period. Twenty replicates were set for each treatment. Control boxes were not exposed to the toxicants. Distilled water was offered to control workers in the Boric acid solution trials. All replicates were set in an incubator (Percival Scientific, USA, temperature: 24.8 ± 0.1 ^{o}C; relative humidity $75.8 \pm 2.8\%$). Mortality was recorded daily for 10 days after initial treatment.

Secondary screening

Amdro, Borax and Boric acid were tested against small laboratory ant colonies consisting of one queen and a hundred workers. Colonies were starved for 3 days prior to the start of the test. Nine to eleven replicates were set for each dose. In another set of experiment, Boric acid was dissolved in 5, 10 and 25% sucrose solution to obtain 0.5 and 1% Boric acid solution. These concentrations of Boric acid were the most promising in the primary screening of oral toxicity. Three doses of Amdro and Borax were considered: 0.3g, 1g and 3.3g. The ants were allowed to feed only on the bait for 48 hrs before adding of the standard laboratory diet of diluted honey and grasshoppers. General observations on the status of the colony and mortality counts (number of dead ants) were recorded daily. The tests continued until the queen, brood, and >90% of the workers were dead, or until the colony recovered and returned to normal state. This condition was considered to be reached after the queen had laid egg and all immature stages were present. Control colonies were not exposed to the toxicant and were fed with the standard laboratory diet of diluted honey and grasshoppers.

Experimental control under semi-field conditions

The experiment was conducted in longitudinal half-barrel sections (90cm x 60cm) filled with top soil in a screened house (average temperature 23.2 ± 2.6 ^{o}C; relative humidity $85.4 \pm 9.7\%$). Colonies of *A. tenella* comprising two queens and nearly 500 workers were introduced into the barrels. Cassava cuttings initially infested with *S. vayssierei* in the field were transplanted in the barrels to reproduce conditions close to those observed in the field. Prior the transplantation of cuttings, the total number of scales per cutting was counted. Colonies were offered grasshoppers at two-day intervals.

The number of ants foraging at the surface of the barrels was counted daily for 3 min, in the morning and in the afternoon, during a three-week period. Then Boric acid-sucrose solution was offered in 11 out of 22 barrels chosen at random. Bait consisted of Boric acid 1% in sucrose

solution 10% and was offered in bait stations, made up with a green plastic cup with large opening at the base for ants to access the bait dispenser. The cup was maintained fixed on the soil by a wooden stick inserted though its bottom. A plastic vial (100 ml) was used as the bait dispenser. A dental roll was inserted via a 2-mm hole located 1 cm from the base of the container. The plastic cup was covered with a funnel to protect the bait container during plant watering. Ants could come and collect the liquid dripping through the dental roll. In the control barrels, bait container were filled with 10% sucrose solution without Boric acid. We monitored ant activity continuously the surface of the barrels for seven weeks. On the seventh week we dug all the barrels to check the status of the queen and the presence of the brood.

Data analysis

For the oral toxicity test, mortality was corrected with the Abbott formula (Abbott 1925) and analyzed with probit transformation (Raymond 1985) to determine time to 50% (LT_{50}) and 90% (LT_{90}) mortality. For ant mortality in the barrel, mean worker activity was compared between pre- and post- treatment period, and between morning and afternoon using the general linear model followed by the Least Square means student's t-test to see which level produced higher or lowest response. Linear regression analysis of workers activity at the surface of the barrels by the time following Boric acid application was performed and slopes were compared between treated and control barrels (Zar 1999). Data were analyzed using SAS software version 9.2 (SAS 2008).

Results

Primary screening

The results of primary screening tests comparing Amdro, Borax and Boric acid are presented on Figure 1. Highest percent mortality of workers was recorded with the 1% Boric acid solution on the tenth day, followed by the 0.5% Boric acid solution, Amdro and Borax. 0.1% Boric acid solution was moderately toxic to *A. tenella* workers.
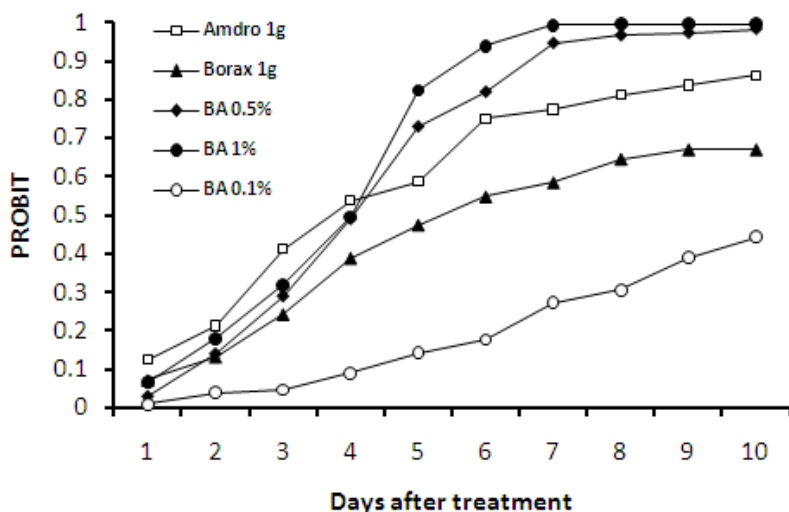
106

Figure 1. Cumulative proportion of workers mortality during primary screening tests.

No significant differences were found between the time to 50% mortality of workers (LT_{50}) for Amdro and Boric acid (0.5% and 1%), but these three did show differences when compared to Borax (6.2 days) and 0.1% Boric acid (10.3 days). Amdro, Borax and 0.1% Boric acid took more time to eliminate 90% of the total ant workers and therefore acted more slowly than Boric acid (0.5% and 1%) (Table 1).

Table 1. LT_{50} and LT_{90} (days) from primary screening tests against of *A. tenella* workers exposed to Amdro, Boric acid and Borax. n= number of ant workers used in the test

Treatment	n	Slope ± SE	LT_{50}(95% CL)	LT_{90}(95% CL)
Amdro (1g)	240	0.25±0.02	4.4(3.6 - 5.0)	9.5(8.5 - 11.1)
Borax (1g)	240	0.21±0.02	6.2(5.4 - 7.0)	12.4(10.8 - 15.1)
Boric acid (0.1%)	300	0.21±0.01	10.3(9.9 - 10.8)	16.2(15.3 - 17.4)
Boric acid (0.5%)	300	0.48±0.04	4.1(3.7 - 4.5)	6.8(6.2 - 7.4)
Boric acid (1%)	300	0.61±0.06	3.6(3.2 - 4.1)	5.8(5.2 - 6.5)

107

Secondary screening

The highest percent reduction of the initial number of workers was recorded with 1% Boric acid solution, followed by 0.5% Boric acid solution, Amdro and Borax. Three colonies exposed to Borax and two exposed to Amdro recovered 3 weeks after exposure and brood developed normally as in the control colonies.

No significant differences were found between the times to 50% mortality of workers (LT_{50}) in all the treatments (2.6-6.9 weeks), with longer delay found with Borax 3.3g (6.9 weeks) and the shorter with Boric acid 1% (2.6 weeks). This was also true for LT_{90} with the exception of Amdro 1g which displayed the shortest time to 90% mortality (6.8 weeks) (Table 2).

Table 2. LT_{50} and LT_{90} (weeks) from secondary laboratory screening tests against *A. tenella* colonies exposed to Amdro, Boric acid and Borax. n= number of ant workers used in the test.

Treatment	n	Slope ± SE	LT_{50}(95% CL)	LT_{90}(95% CL)
Amdro (0.3g)	400	0.27±0.02	5.9(5.5-6.4)	10.6(9.5-12.1)
Amdro (1g)	400	0.37±0.08	3.4(2.3-5.1)	6.8(5.1-15.7)
Amdro (3.3g)	400	0.18±0.04	3.5(2.0-4.6)	10.5(8.1-18.4)
Borax (0.3g)	400	0.33±0.03	6.9(6.3-7.8)	10.8(9.5-12.9)
Borax (1g)	500	0.26±0.06	3.1(1.8-4.6)	8.0(7.5-13.4)
Borax (3.3g)	500	0.18±0.05	4.7(3.8-5.8)	9.2(8.3-20.8)
Boric acid (0.1%)	400	0.26±0.05	6.2(4.9-9.6)	11.0(15.3-17.4)
Boric acid (0.5%)	400	0.29±0.06	4.3(3.3-6.2)	8.8(6.7-17.4)
Boric acid (1%)	750	0.21±0.03	2.6(1.5-3.4)	8.8(7.1-13.2)

Bait made up of Boric acid and 10% sucrose significantly reduced LT_{50} and LT_{90} in *A. tenella* colonies in the laboratory (Table 3). There were no significant difference in LT_{50} for the three sugar concentrations and the 0.5% Boric acid. The same was true for LT_{90}. Also, there was no significant difference in LT_{50} for the three sugar concentrations with 1% Boric acid. The same was also true for LT_{90}.

108

Table 3. LT_{50} and LT_{90} (weeks) from secondary laboratory screening tests against *A. tenella* colonies with Boric acid-sucrose solution. n= number of ant workers used in the test

Boric acid	Sugar	n	Slope ± SE	LT_{50}(95% CL)	LT_{90}(95% CL)
0.5%	5%	900	0.48±0.04	3.7(3.3-4.0)	6.4(5.8-5.4)
	10%	900	0.46±0.07	2.8(1.8-3.5)	5.6(4.6-5.9
	25%	800	0.32±0.01	3.1(2.9-3.2)	7.1(6.8-7.4)
1 %	5%	800	0.44±0.02	3.4(3.2-3.7)	6.3(5.9-6.9)
	10%	1000	0.44±0.02	2.9(2.7-3.1)	5.8(5.5-6.2)
	25%	1100	0.43±0.02	3.0(2.8-3.3)	6.0(5.6-6.5)

Experimental control under semi-field conditions

Before the application of Boric acid sucrose solution, no difference was observed in mean workers activity between barrels that served as control and the barrels that received the boric acid treatment application (control group: 6.62 ± 0.74 workers/3min; treatment group: 6.57 ± 0.74 workers/3min; comparison control vs treatment: ($t = 0.02$; df = 10; p =0.98). There was a significant difference between activities in the morning compared to that in the afternoon in control group ($F_{(1,757)}$=24.78; p<0.0001) and treated groups ($F_{(1,757)}$=19.40; p<0.0001). The application of Boric acid to ant colonies significantly reduced the ant activity at the surface of the treated barrels (after the treatment: 1.51 ± 0.74 workers/3min; comparison before vs after treatment: t = 7.38; df = 12; p <0.001) (Figure 2). This activity decreased continuously four weeks after the treatment and the regression slope was significantly different from that of the control (t = 3.09; df = 10; p = 0.05). The activity in the control barrel remained unchanged (t = 0.76; df = 10; p = 0.45), but there were again difference between the activity in the morning and in the afternoon (t = 5.23; df = 10; p <0.001). In the treated barrels we recorded the complete loss of four colonies. The remaining barrels had queens with reduced number of workers. No significant difference was found between the number of scale insect at the end of the experiment compared to the initial number in both treated and control barrels. However, only dead individuals were recorded on cuttings in the colonies that were decimated.
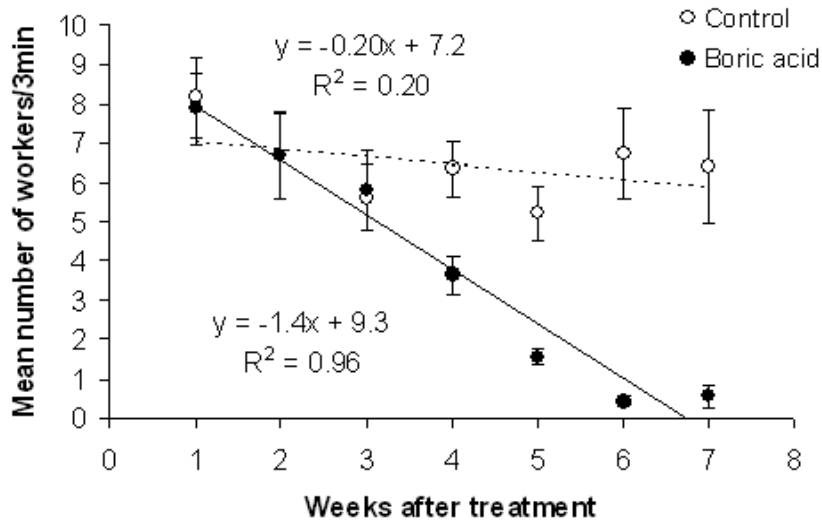
Figure 2. Ant activity at the surface of the barrel in the screenhouse in the morning and in the afternoon. Each data point represents the mean activity at the surface of 11 barrels.

Discussion

There presently a complete lack of effective chemical control methods for the control of the pest ant *Anoplolepis tenella* in agricultural areas. The control of the congeneric species *A. gracilipes* can be achieved through broadcasting of granulated Presto 01[TM] ant bait, with Fipronil (0.1 g/kg) as the active ingredient on the forest floor. Within 11 weeks, ant activity on the ground was reduced by 98-100% (Abbott and Green 2007). However, we considered that Presto 01[TM] which is a fish meal bait matrix may not be adapted to a species mainly feed on scale exudates. The results presented here suggest that Amdro, Borax and Boric acid solution have a delayed toxicity on *A. tenella* colonies. Late toxicity is an important attribute of candidate toxicants to be incorporated into ant baits in addition to the fact that it should not be repellent. In developing methods for the control of the red imported fire ant *Solenopsis invicta,* delayed toxicity was defined as the mortality of less than 15% of the workers tested at 24h and more than 80% after day 14 (Stringer et al. 1964). In this study, time to 50% reduction of workers was estimated between 1-5 days. This time was considered sufficient for the bait to spread in the colony. Because toxicants are diluted during trophallaxis, delayed toxicity is an extremely important component of an effective bait to control ant populations. Workers must survive long enough to repeatedly feed on the bait and return to the colony (Rust et al. 2004).

Boric acid solutions were more promising in killing ant workers than Amdro and Borax, especially when dissolved into sucrose solution. The low mortality observed in Amdro and Borax can be attributed to their solid formulation which can cause differences in feeding preference of *A. tenella*. Also, Amdro and Borax may have displayed deterred feeding as observed in colonies of red imported fire ant exposed to higher concentration of Amdro (Klotz et al. 1996). Liquid Boric acid-sucrose solution exploited the natural feeding habits of sweet-eating ants that collect honeydew or nectar (Klotz and Williams 1996). This was similar to the feeding habit of *A. tenella* given that honeydew collected from hemipteran insects, especially *Stictococcus vayssierei,* constitutes the main component of *A. tenella*'s diet (Fotso Kuate et al. 2008).

Low concentrations of Boric acid are known not to be repellent to a variety of ant species including *Camponotus floridanus* (Klotz and Moss 1996), *Monomorium pharaonis*, *Tapinoma melanocephalum* as well as the Argentine ant (Klotz et al. 1996). While the concentration of Boric acid is too high in most available commercial baits, at low concentrations (e.g., 1% Boric acid in 10% sugar-water) it is extremely effective at killing laboratory colonies of *Monomorium pharaonis, Tapinoma melanocephalum, Solenopsis invicta* and *L. humile* (Klotz and Williams 1996; Klotz et al. 1997b; Ulloa-Chacon and Jaramillo 2003). This was also observed with *A. tenella* colonies in this study.

Successful control of *A. tenella* in the laboratory with Boric acid-sucrose solution is a promising indicator for the development of specific bait against this pest ant in agricultural areas. There are some advantages related to the Boric acid-based water bait as it provides moisture and exploit the liquid feeding habits of honeydew-collecting ant. Boric acid may also cause the disruption of water regulation, thus increasing bait consumption to counterbalance dehydration (Klotz and Moss 1996; Klotz et al. 1996). The next step is to determine whether these results will be consistent if Boric acid sucrose solution is tested on large colonies of *A. tenella* in the field. There is however clear indication from the screenhouse experiment that successful control can be achieved in infested cassava fields.

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General Discussion and conclusion

Summary of previous chapters

In the first chapter, we used tree complementary techniques (quadrat, pitfall and baiting) to sample ants in the three vegetation types (forest, fallow and mixed-crop fields) prevailing in southern Cameroon. We recorded two hundred and fifty four ant morphospecies grouped in 10 subfamilies and 44 genera. *Anoplolepis tenella* was the second most abundant species after *Myrmicaria opaciventris*. Quadrat sampling yielded more species than the two other methods and baiting was the most redundant method. Ant diversity was higher in the forest compared with mixed-crop field. *A. tenella* displayed positive interaction with *Technomyrmex parandrei* and negative interaction with *Myrmicaria opaciventris.*

In chapter two, we demonstrated that ant species richness, abundance, density, activity and the composition were affected by vegetation type and season. Seasonal variation in species composition was observed in the mixed-crop fields. Forests displayed a relative stability of climatic factors which limit variation in ant species between seasons. *Anoplolepis tenella* abundance, density and activity were significantly higher in mixed-crop fields compared with forests and fallows. Its density and activity was affected by season and temperature, relative humidity and soil characteristics.

In chapter three, we found that honeydew producers and plants offering nectar were among possible mechanism structuring ant assemblage in the humid forest zone of southern Cameroon. Resources (nectaries and honeydew) were monopolized by ant species either through numerical dominance (*Technomyrmex lujae* and *Oecophylla longinoda*) or construction of shelter (*Crematogaster* sp1and *Anoplolepis tenella*). Most association between ant species and hemipteran insects appeared to be non-obligate and diffuse, with many ant species interacting with many honeydew producers. However a higher specialization index was observed for *A. tenella* and *Stictococcus vayssierei. Anoplolepis tenella* was rare on nectar and this strengthened its specific association with *S. vayssierei.*

In chapter four, we demonstrated the active role of *A. tenella* workers in the transport and dissemination of *S. vayssierei* mobile stages within plant and from one plant to another. We found that the rate of dispersal increased with increasing ant density and no case of phoresis was

observed with *A. tenella* queens during nuptial flight; neither did the wind dispersal of scale crawlers observed in the field.

In chapter five, we demonstrated that Boric Acid, Amdro and Borax had a lethal effect on laboratory colonies of *A. tenella*. A 1% Boric acid-sucrose solution caused significant mortality in *A. tenella* with LT_{50} and LT_{90} estimated between 3 and 6 weeks.

Discussion

Here I present a general discussion on *Anoplolepis tenella* ecology using results from the experiments we conducted and further information from previous observations and literature. I discuss two statements that prompted by this study on the ecology of *A. tenella* and its association with *S. vaysserei*. These are:

i)   *A. tenella* distribution and abundance is affected by vegetation type, subsequent to disparities among biotic and abiotic factor between these vegetations

ii)   Honeydew composition and physiological adaptation in ants excludes some species from maintaining association with honeydew producers while others species like *A. tenella* are favored.

i) *Anoplolepis tenella* distribution and abundance is affected by vegetation type, subsequent to disparities among biotic and abiotic factors between these vegetations.

This work outlined that in the humid forest zone of southern Cameroon, the type of vegetation significantly affects the distribution of ant species. From the data collected, forest plots had greater species richness compared with fallow and mixed-crop field. This is a generalized pattern observed in most studies on the distribution of invertebrates and mostly insects. The habitat that has been subjected to anthropogenic disturbance like the mixed-crop field generally displays low species diversity (Beck et al. 2002; Bruehl and Eltz 2010). Several explanations have been given among which the change in vegetation structure, the change of microclimatic factors that may favor thermophilic species, the inability of some species to colonize the new environment (Dolek et al. 2009). In southern Cameroon, mixed-crop fields are established after complete clearance and burning of preexisting vegetation. This action induces changes in microclimatic factors such as the increase of soil temperature because of bare land, which will continuously change in

relation to the covering by the growing crop. Fallows and forests which display a relative stability in their ecological features appear to be more suitable for biodiversity conservation. The stability of ecological factors goes along with the diversity and availability of food sources such as extrafloral nectaries (EFN) and honeydew from hemipteran insects, which are often invoked as possible mechanisms structuring ant communities, hence the greater ant diversity in the forests.

The effect of vegetation type was more pronounced on *A. tenella* distribution and abundance with greater abundance, density and activity in mixed-crop fields. Studies on *A. tenella* nest distribution showed that nests were in most cases located at the base of scale infested crop plants, mainly cassava (94%), implying the existence of factor influencing their selection for site nesting. In this case the presence of *Stictococcus vayssierei* under these plants could be the determinant factor since the ant feed on the scale honeydew (Fotso Kuate et al. 2006). The agronomic practice which consists in a gradual replacement of forests by mixed-crop fields dominated by cassava and others scale host plants creates new niches for the scale and its associated ant and consequently increases nest density. After harvesting, the land is left to a restorative period (fallow) where left-over cassava stems persist and remain the main host for scale population while the fallows mature. Neither cassava nor other cultivated scale host plants are available in the forest. Only wild and less infested host plants can be found (Tindo et al. 2009). In this less disturbed environment with low scale density or their absence on plants, niches for *A. tenella* are relatively rare resulting in low nest density and low abundance. This hypothesis of the existence of determinism in the choice of nesting site is also confirmed by the aggregated spatial distribution observed in mixed-crop fields (Fotso Kuate et al. 2006), which indicates the existence of certain constraints in the environment that would guide population to places suitable for their fitness (Pemberton and Frey 1984). The aggregation also results in a selective behavior on the part of individuals, leading them to establish energy associated with a particular nest site, and adopting one that allows them to reduce energy costs associated with the movement. In *Dolichoderus* for example, when the distance between the nest and foraging site is distant for facilitating the transport of harvested resources, the whole colony migrates en masse to settle in the harvesting site (Hölldobler and Wilson 1990). The presence of nests of *A. tenella* in secondary forest and in primary forest (in the absence of *S. vayssierei*) suggests that the close relationship between the presence of scale and that of the ant found in the fields would be a

secondary adaptation for *A. tenella*. *A.tenella* during foraging may have gradually migrated from the forest to farmland, with the forest remaining as a reservoir considering the abundant quantity of cocoons that is found in the litter (Fotso Kuate et al. 2006). Moreover mutualism between ants and their hemipteran partners may lead to extensive co-adaptations, especially behavioral changes among ants. This is the case of ants carrying their scale trophobionts and placing them on appropriate places on the plant (Way 1963; Hölldobler and Wilson 1990), or new gynes who carry their trophobionts between the mandibles during mating flight to provide a new source of honeydew to the new growing colony (Gullan and Kosztarab 1997; Williams 1997). *Anoplolepis tenella* presently carries its associated scale and is therefore likely the main cause of the spread of *S. vayssierei*.

ii) Honeydew composition and physiological adaptation in ants excludes some species from maintaining association with honeydew producers while others species like *A. tenella* are favored.

There is a broad range of interactions between species living in the same environment and general theories and mechanism of beneficial interactions among unrelated organisms are summarized by Stadler and Dixon (2008) modified after Yu (2001). Among them we have the by-product mutualism. This theory is defined as a selfish activity by one partner, which unintentionally creates an indirect benefit for the other partner that outweighs the cost of the selfish act. This definition is exemplified by the tending activity of ants on hemipteran insects, mainly aphids and coccids (Way 1963; Pierce et al. 2002).

From consumer's perspective, food quality and quantity can influence foraging decision. Ants foraging for carbohydrates are mainly attracted by mono-and disaccharides. Ants that visit EFN are attracted by the monosaccharide fructose and glucose. Some ant-plants produce the disaccharide sucrose that is attractive to generalist ant species. Therefore ants attracted to sucrose must have high invertase activity in their digestive tract to be able to cleave sucrose molecules. Species like *Lasius niger* and *Myrmica rubra* prefer disaccharide sucrose to monosaccharide glucose and fructose, which they can manage with invertase from their mandibular glands (Ricks and Vinson 1972).

From this statement, we could speculate about the utilization of *S. vayssierei* attendance by ants to understand why some ant species are attracted and others are not. We could formulate two hypotheses:

(1) Honeydew produced by *S. vayssierei* is sucrose-free and *A. tenella* doesn't have invertase activity in its digestive track. This has been verified in *Pseudomyrmex* ants that live on *Acacia* and specialize in the sucrose free EFN (Heil et al. 2005). In this case, nectar produced by ant plants is chemically custom-made to attract and fit the need of the mutualistic ants and at the same time is made less attractant to others ant species that are considered as potential exploiters (Heil et al. 2010). For instance, EFN produce by these plant possess a level of invertase activity that is enough to obtain a post secretory hydrolyses of sucrose so that the attracted ant can easily feed on the product of the hydrolysis (Heil et al. 2005). This could be the case for scale honeydew and *A. tenella*.

(2) Honeydew produced by *S. vayssierei* contains sucrose and no invertase activity. In this case, attracted ant should possess invertase in their digestive tract to cleave the sucrose molecules. Invertase is known to be either lacking or present at low concentrations in honeydew-feeding ants (Ayre 1967), and other oligosaccharide-hydrolyzing enzymes are believed to be absent or in low concentrations in many ants (Boeve and Wackers 2003). Therefore, much of the energy present in honeydew may not be accessible to many ant species as demonstrated in *Dolichoderus* species (Cook and Davidson 2006).

Conclusion

The aim of this thesis was to highlight some aspects of the biology and ecology of the ant *Anoplolepis tenella* that can be useful in the development of control option against the African root and tuber scale *Stictococcus vayssierei* in central Africa. Although ants perform important ecological function, their role in the outbreak of pests has been mainly focused on invasive ant. The framework of the present study presented a fascinating case where a native ant species is associated with the proliferation on and indigenous scale pest insect. In this thesis, I studied the distribution of *A. tenella* and co-occurring ant species in dominant vegetation types. I examined some of the factors that could explain the observed distribution. I assessed the interaction between ant species, honeydew producers and plants offering extrafloral nectaries. I demonstrated the active role of *A. tenella* in the dispersal of *S. vayssierei* and initiated control

measures in the laboratory. In this way, I hope to have contributed to our understanding of *A. tenella* ecology in southern Cameroon and the larger humid forest zone of Central Africa.

The two hypotheses stated at the end of the discussion on honeydew composition need to be verified in order to complement our understanding of the interaction between *Anoplolepis tenella* and *Stictococcus vayssierei*. This information is also needed to develop specific bait for *A. tenella* that will use sugar and amino acid found in scale honeydew as attractant to make the formulated bait more competitive in the field. We could then plan for large scale control of *A. tenella* in the fallows in scale infested area to reduce scale abundance and damage to the crop. If this is achieved, we would have contributed to poverty alleviation in the humid forest zone of Central Africa.

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124

Annexes

Annex 1: List of ant morphospecies recorded in three vegetation types in southern Cameroon. Numbers in the table represent the total occurrence (pseudo-abundance) of each species.

Subfamilies and species	Fallow	Forest	Mixed-crop	Total
Aenictinae				
Aenictus decolor	2	1	4	7
Aenictus congolensis	4	2	3	9
Amblyoponinae				
Amplyopone pluto		1		1
Cerapachyinae				
Cerapachys sp1	1	4	1	6
Cerapachys sp2		1		1
Cerapachys sp3		1		1
Dolichoderinae				
Tapinoma carininotum	134	10	225	369
Tapinoma luridum	4	11	1	16
Tapinoma Taylor sp T2	6	2		8
Technomyrmex (Engramma) kohli	3	17		20
Technomyrmex (Engramma) laurenti		1		1
Technomyrmex (Engramma) lujae		55		55
Technomyrmex moerens	8	23	1	32
Technomyrmex pallipes	20	13		33
Technomyrmex parandrei	191	330	12	533
Technomyrmex sp9			1	1
Dorylinae				
Dorylus (Alaopone) conradti	1	1	2	4
Dorylus (Anomma) gribodoi	43	43	22	108
Dorylus (Anomma) sjoestedti	18	42	51	111
Dorylus (Anomma) titan	14	19		33
Formicinae				
Anoplolepis tenella	282	216	454	952
Camponotus (Myrmachraphe) furvus	3	2		5
Camponotus (Myrmachrhaphe) tameri	9		3	12
Camponotus (Myrmisolepis) maynei	7			7
Camponotus (Myrmosaga) schoutedeni	20		20	40
Camponotus (Myrmosericus) flavomarginatus	138	1	204	343
Camponotus (Myrmotrema) bayeri	13	4	1	18
Camponotus (Myrmotrema) foraminosus	1			1
Camponotus (Myrmotrema) foraminosus flavus	3		1	4
Camponotus (Myrmotrema) haereticus	155	12	37	204
Camponotus (Myrmotrema) olivieri gp	8	14		22
Camponotus (Paramyrmamblys) simus	2			2
Camponotus (Tanaemyrmex) agonius	21	1	23	45
Camponotus (Tanaemyrmex) brutus	136	52	17	205
Camponotus (Tanaemyrmex) donisthorpei	2	1	3	6

Subfamilies and species	Fallow	Forest	Mixed-crop	Total
Camponotus (Tanaemyrmex) langi	2	21	2	25
Camponotus (Tanaemyrmex) sp (in brutus gp)		1	1	2
Camponotus (Tanaemyrmex) varus			2	2
Camponotus chrysurus s.s	38	33	24	95
Camponotus spC		1		1
Camponotus spD		1		1
Camponotus spH		1	1	2
Camponotus vividus	3	4		7
Camponotus(Tanaemyrmex) acvapimensis	105	2	160	267
Camponotus(Tanaemyrmex) maculatus	133	50	209	392
Camponotus(Tanaemyrmex) wellmani	2	3	1	6
Lepisiota cacozela	7	6	5	18
Lepisiota crinita Cameroun form			4	4
Lepisiota sp3	2		11	13
Lepisiota sp4		1	3	4
Lepisiota sp5	1		17	18
Oecophylla longinoda	44	42	3	89
Paratrechina incallida	9	4		13
Paratrechina sp Gabon		2		2
Paratrechina weissi	96	13	270	379
Plagiolepis alluaudi	1			1
Polyrhachis aerope	48	2	2	52
Polyrhachis curta		2		2
Polyrhachis decellei		1		1
Polyrhachis decemdentata	36	12	2	50
Polyrhachis laboriosa	27	5	2	34
Polyrhachis militaris	34	78	5	117
Polyrhachis phidias		1		1
Polyrhachis rufipalpis	4	13	2	19
Polyrhachis sulcata	1			1
Polyrhachis volkarti		3		3
Polyrhachis weissi		5		5
Polyrhachis wellmani	5	7		12
Pseudolasius sp2	1	7		8
Pseudolasius weissei	1			1
Myrmicinae				
Atopomyrmex mocquerysi	1	5		6
Calyptomyrmex sp1		1		1
Calyptomyrmex sp2		1		1
Cardiocondyla shuckardi			4	4
Cardiocondyla weserka	3		4	7
Cataulacus erinaceus	6	14	1	21
Cataulacus guineensis	59	27	3	89
Cataulacus huberi	11	19		30
Cataulacus jeanneli	2			2

Subfamilies and species	Fallow	Forest	Mixed-crop	Total
Cataulacus kohli	1			1
Myrmicinae				
Cataulacus moquerysi		1		1
Cataulacus pygmaeus	7			7
Cataulacus sp1	2	14		16
Cataulacus sp12	1	1		2
Cataulacus sp7	4	2		6
Cataulacus spB		1		1
Cataulacus taylori	5	2	1	8
Cataulacus traegaordhi	1	3		4
Cataulacus weissei	3	2		5
Crematogaster (Atopogyne) africana variety	29	10		39
Crematogaster (Atopogyne) batesi	1	2		3
Crematogaster (Atopogyne) cuvierae	4	3		7
Crematogaster (Atopogyne) wasmanni	2	18		20
Crematogaster (Cr.) acis	18		1	19
Crematogaster (Cr.) excisa s.s.	2	4	2	8
Crematogaster (Cr.) inconspicua	13	23	8	44
Crematogaster (Cr.) menilekii	4	14		18
Crematogaster (Cr.) ochraceiventris	1		2	3
Crematogaster (Cr.) painei	3	3		6
Crematogaster (Cr.) stigmata	9	10		19
Crematogaster (Decacrema) costeboriensis	8	6		14
Crematogaster (Decacrema) lango	2	2		4
Crematogaster (Nematocrema) stadelmanni	25	14	1	40
Crematogaster (Orthocrema) pauciseta		2		2
Crematogaster (Oxygyne) n sp ? cf oscaris	2			2
Crematogaster (Sphaerocrema) concava	15	2		17
Crematogaster (Sphaerocrema) gabonensis	18	7	6	31
Crematogaster (Sphaerocrema) kneri	2	3		5
Crematogaster (Sphaerocrema) luctans sordidoides	6	7		13
Crematogaster (Sphaerocrema) ochraceiventris		5		5
Crematogaster (Sphaerocrema) striatula	132	106	19	257
Crematogaster (Sphaerocrema) wellmani	2			2
Crematogaster (Sphaerocrema) zavattarii	51	53	2	106
Crematogaster clariventris	19	6	8	33
Decamorium uelense	4	4	2	10
Meranoplus inermis	15		8	23
Monomorium altinode			1	1
Monomorium angustinode	16		23	39
Monomorium bicolor	2		90	92
Monomorium egens	11	4	10	25
Monomorium gabrielense	1	4	1	6
Monomorium guineense	8	15	7	30
Monomorium tynsorum	8	1	19	28

Subfamilies and species	Fallow	Forest	Mixed-crop	Total
Monomorium vaguum	10	2	37	49
Myrmicinae				
Myrmicaria opaciventris	418	33	576	1027
Oligomyrmex (Aneleus) silvestrii		1		1
Oligomyrmex diabolus	1		1	2
Oligomyrmex n sp	49		13	62
Pheidole corticicola	5	6	19	30
Pheidole dea	2	30	5	37
Pheidole megacephala	10	1	50	61
Pheidole nigeriensis	99	96	59	254
Pheidole nsp	29	38	64	131
Pheidole occipitalis	36	32	47	115
Pheidole philippi	1	5	4	10
Pheidole pulchella	2	25	10	37
Pheidole pusilla		17		17
Pheidole retronitens	7	10	13	30
Pheidole saxicola		2	3	5
Pheidole schultzei	23	9	32	64
Pheidole sculpturata	1			1
Pheidole senilifrons	2		2	4
Pheidole sp16			2	2
Pheidole speculifera	12	95	8	115
Pheidole squalida	26	15	59	100
Pheidole stephensi	4	21	5	30
Pheidole tenuinodis	31	77	41	149
Pheidole tenuinodis			10	10
Pheidole termitophila	35	19	28	82
Pheidole thysvillensis	44	38	53	135
Pheidole welgelegenensis	5	3	9	17
Prionopelta sp1	3	2		5
Prionopelta sp2		1		1
Pyramica sistrurus		2		2
Pyramica sp1	12	8	2	22
Pyramica sp2	1	1		2
Pyramica sp3			1	1
Pyramica sp4		1		1
Pyramica sp5		1		1
Rhopthromyrmex opacus	5		3	8
Strumygenys sp1	3	3	3	9
Terataner luteus	2			2
Terataner velatus	2	1		3
Tetramorium (Triglyphothrix) brevispinosum		6		6
Tetramorium (Triglyphothrix) cf cryptica	4	12		16
Tetramorium (Triglyphothrix) cf minimum		3	1	4
Tetramorium (Triglyphothrix) monardi		4		4

128

Subfamilies and species	Fallow	Forest	Mixed-crop	Total
Tetramorium (Triglyphothrix) n sp		3		3
Myrmicinae				
Tetramorium (Xiphomyrmex) angulinode	58	6	155	219
Tetramorium (Xiphomyrmex) angulinode type form	3		5	8
Tetramorium (Xiphomyrmex) guineense	3	5		8
Tetramorium aculeatum	63	23	3	89
Tetramorium angulinode Congo form	1	10		11
Tetramorium anxium	3	2		5
Tetramorium cf pylacum	3	5	2	10
Tetramorium coloreum	24	15	1	40
Tetramorium dumezi		9		9
Tetramorium guineense	10	52	1	63
Tetramorium jugatum	7	2	5	14
Tetramorium lucayanum	3	3	8	14
Tetramorium magnificum	4	178	3	185
Tetramorium n sp cf magnificum	1	31	2	34
Tetramorium occidentale	16	3	2	21
Tetramorium peutli	1	7		8
Tetramorium quadridentatum	9	8		17
Tetramorium sericeiventre	2		54	56
Tetramorium simillimum	30	16	79	125
Tetramorium sp12	1	5		6
Tetramorium sp14		4		4
Tetramorium sp17	1	1		2
Tetramorium sp18	1			1
Tetramorium sp5	1	6	5	12
Tetramorium sp7	3		1	4
Tetramorium spB			1	1
Tetramorium spP		1		1
Tetramorium susannae	3			3
Tetramorium unicum	1	1	1	3
Ponerinae				
Anochetus africanus	29	54	18	101
Anochetus bequaerti	2	8		10
Anochetus katonae		5		5
Anochetus n sp		3		3
Anochetus traegaordhi	1	5	3	9
Centromyrmex sp2	1	3		4
Centromyrmex sp3		3		3
Cryptopone sp1			1	1
Hypoponera brevis	2	2		4
Hypoponera coeca	16	7	9	32
Hypoponera intermedia	1	1	3	5
Hypoponera rothkirchi	6	8	1	15
Leptogenys conradti	3	2		5

Subfamilies and species	Fallow	Forest	Mixed-crop	Total
Leptogenys sp1	2	4		6
Ponerinae				
Leptogenys spA		1		1
Odontomachus assiniensis	76	91	25	192
Odontomachus troglodytes	115	140	94	349
Pachycondyla (Bothroponera) sjostedti	2	1		3
Pachycondyla (Mesoponera) escherichi	6	2	8	16
Pachycondyla (Mesoponera) ingesta	62	21	24	107
Pachycondyla (Xiphopelta) ambigua	74	20	37	131
Pachycondyla (Xiphopelta) testacea	4	4	2	10
Pachycondyla modesta		6		6
Pachycondyla pongarensis	6	11	4	21
Pachycondyla soror	20	72	5	97
Pachycondyla sp2	7	2		9
Pachycondyla sp8	1			1
Pachycondyla tarsata	42	327	128	497
Phyrnoponera armata		12		12
Phyrnoponera gabonensis		7		7
Plathytyrea sp2		1		1
Platythyrea conradti	1	3		4
Platythyrea modesta	9	15		24
Plectroctena gabonensis		4	2	6
Proceratiinae				
Probolomyrmex guineensis	1			1
Dyscothyrea sculptior	1			1
Pseudomyrmecinae				
Tetraponera aethiops		12		12
Tetraponera latifrons		1		1
Tetraponera lepida	64	4	6	74
Tetraponera nasuta		7		7
Tetraponera ophtalmica	1			1
Total	4079	3507	3893	11479

Annex 2: Ant species feeding on extrafloral nectaries (EFNs), floral nectaries (FNs), and honeydew, their vegetation and activity. Numbers are frequencies of spatially independent occurrences or interactions with different plant species. The last column shows the number of plant species visited for nectar.

Ant species	Vegetation			Resources			
	Fallow	**Forest**	**Mixed**	**EFN**	**FN**	**Honeydew**	**Plants**
Formicinae							
Anoplolepis tenella	34	3	137	2	0	172	2
Camponotus chrysurus	5	0	1	4	0	3	5
Camponotus (Myrmosericus) flavomarginatus	11	1	13	15	0	10	5
Camponotus (Tanaemyrmex) brutus	11	1	1	9	3	5	5
Camponotus (Myrmotrema) haereticus	13	4	1	15	4	5	8
Camponotus(Tanaemyrmex) acvapimensis	42	1	8	31	7	25	9
Camponotus(Tanaemyrmex) maculatus	7	3	4	9	1	6	5
Camponotus (Myrmosaga) schoutedeni	1	0	0	0	2	1	0
Camponotus sp10	1	0	1	1	0	2	1
Camponotus (Myrmotrema) foraminosus	1	0	0	1	0	0	1
Camponotus (Myrmachrhaphe) tameri	1	0	0	1	0	0	1
Camponotus (Tanaemyrmex) donisthorpei	1	0	0	0	0	1	0
Camponotus sp17	1	0	0	1	1	0	1
Camponotus (Myrmotrema) bayeri	2	0	0	2	1	0	2
Camponotus spH	1	0	0	1	0	0	1
Lepisiota sp3	0	1	0	1	0	0	1
Lepisiota sp4	0	1	0	1	0	0	1
Oecophylla longinoda	16	12	1	24	5	14	7
Paratrechina weissi	1	3	1	4	1	2	3
Paratrechina incallida	0	1	0	1	0	0	1
Polyrhachis aerope	9	1	1	11	1	0	5
Polyrhachis decemdentata	2	2	0	3	0	2	2
Polyrhachis laboriosa	9	0	0	8	2	1	4
Polyrhachis lanuginosa	0	1	0	1	0	0	1
Polyrhachis militaris	1	7	2	8	2	4	8
Polyrhachis rufipalpis	0	1	0	1	0	0	1
Polyrhachis wellmani	1	6	0	6	0	2	5
Pseudolasius weissei	1	0	0	0	0	1	0
Myrmicinae							
Atopomyrmex mocquerysi	0	1	0	0	0	1	0
Cataulacus sp2	1	3	0	3	1	0	3
Cataulacus traegaordhi	8	2	0	1	0	0	1
Cataulacus guineensis	1	0	0	4	0	2	4
Cataulacus nr guineensis	3	0	0	1	0	0	1
Cataulacus kohli	1	0	0	0	1	0	2
Cataulacus huberi	2	3	0	0	1	0	4
Cataulacus guineensis	1	0	0	0	1	0	6
Cataulacus pygmaeus	1	0	1	0	0	0	1
Crematogaster clariventris	9	2	1	8	3	7	4
Crematogaster (Sphaerocrema) striatula	56	66	5	68	14	82	20
Crematogaster (Nematocrema) stadelmanni	11	3	0	10	2	7	8

Ant species	Vegetation			Resources			
	Fallow	**Forest**	**Mixed**	**EFN**	**FN**	**Honeydew**	**Plants**
Crematogaster (Sphaerocrema) zavattarii	12	11	3	17	1	12	8
Crematogaster (Cr.) inconspicua	10	7	0	11	1	9	7
Crematogaster (Sphaerocrema) luctans	3	0	1	1	0	3	1
Crematogaster (Sphaerocrema) gabonensis	10	0	0	9	3	2	4
Crematogaster (Cr.) excisa s.s.	0	4	0	1	1	3	1
Crematogaster (Sphaerocrema) kneri	0	3	0	3	0	1	3
Crematogaster (Cr.) ochraceiventris	0	1	0	1	0	1	1
Crematogaster (Orthocrema) pauciseta	0	6	0	2		5	2
Crematogaster (Atopogyne) africana	10	11	1	10	2	15	8
Crematogaster (Decacrema) costeboriensis	2	3	0	2	0	3	2
Crematogaster (Decacrema) lango	3	1	0	2	1	3	2
Crematogaster (Cr.) painei	0	1	1	1	0	1	1
Crematogaster (Cr.) menilekii	3	2	0	4	0	2	4
Crematogaster (Atopogyne) wasmanni	7	2	0	8	2	2	5
Crematogaster (Atopogyne) cuvierae	6	6	0	9	1	5	7
Crematogaster (Atopogyne) batesi	0	1	0	1	0	0	1
Crematogaster (Cr.) acis	0	3	0	2	0	1	2
Monomorium bicolor	0	0	4	0	0	4	0
Monomorium vaguum	0	1	1	1	0	2	1
Monomorium gabrielense	0	5	0	4	0	1	4
Myrmicaria opaciventris	26	11	30	45	5	26	14
Pheidole pulchella	0	1	0	1	0	0	1
Pheidole occipitalis	4	0	1	5	1	1	2
Pheidole nigeriensis	1	0	0	0	0	1	0
Pheidole dea	0	2	0	1	0	2	1
Pheidole nsp	8	6	4	12	4	7	6
Pheidole termitophila minor	2	1	0	2	1	1	2
Pheidole stephensi	2	3	0	2	21	5	3
Pheidole senilifrons minor	0	0	1	0	0	1	0
Pheidole squalida minor	4	3	0	3	0	5	2
Pheidole tenuinodis minor	0	3	1	3	0	4	2
Pheidole sp15	2	0	0	1	1	1	1
Pheidole sp16	0	0	5	1	1	4	1
Pheidole speculifera	0	0	2	0	0	2	0
Rhoptromyrmex opacus	0	0	2	2	0	0	2
Serrastruma sp1	0	1	5	1	0	5	1
Tetramorium (Xiphomyrmex) angulinode	0	1	0	1	0	0	1
Tetramorium simillimum	0	0	1	0	0	1	0
Tetramorium sp5	0	2	0	0	0	2	0
Tetramorium quadridentatum	1	0	0	1	0	0	1
Tetramorium aculeatum	20	18	1	23	4	22	11
Tetramorium guineense	0	1	0	1	0	1	2
Tetramorium longicorne	0	0	1	0	0	1	0
Tetramorium magnificum	0	18	0	16	0	6	5
Tetramorium dumezi	0	1	0	1	0	0	1
Tetramorium (Triglyphothrix) monardi	0	2	0	0	0	2	0

Ant species	Vegetation			Resources			
	Fallow	**Forest**	**Mixed**	**EFN**	**FN**	**Honeydew**	**Plants**
Dolichoderinae							
Tapinoma carininotum	8	3	0	9	2	5	5
Technomyrmex parandrei	0	2	0	1	0	1	1
Technomyrmex pallipes	3	1	0	4	0	0	3
Technomyrmex (Engramma) kohli	0	12	0	6	1	7	3
Technomyrmex pallipes	1	1	0	1	0	1	1
Technomyrmex (Engramma) lujae	4	49	0	19	4	42	12
Technomyrmex pallipes	0	0	1	1	0	0	1
Technomyrmex moerens	1	3	0	3	0	3	3
Technomyrmex sp9	1	0	0	1	1	0	1
Ponerinae							
Odontomachus assiniensis	0	4	0	2	0	2	2
Odontomachus troglodytes	0	8	0	7	0	3	5
Pseudomyrmecinae							
Tetraponera lepida	12	4	0	15	2	2	8
Tetraponera ophtalmica	1	0	0	1	0	1	1
Total (median)	**433**	**358**	**244**	**537**	**113**	**597**	**(2)**
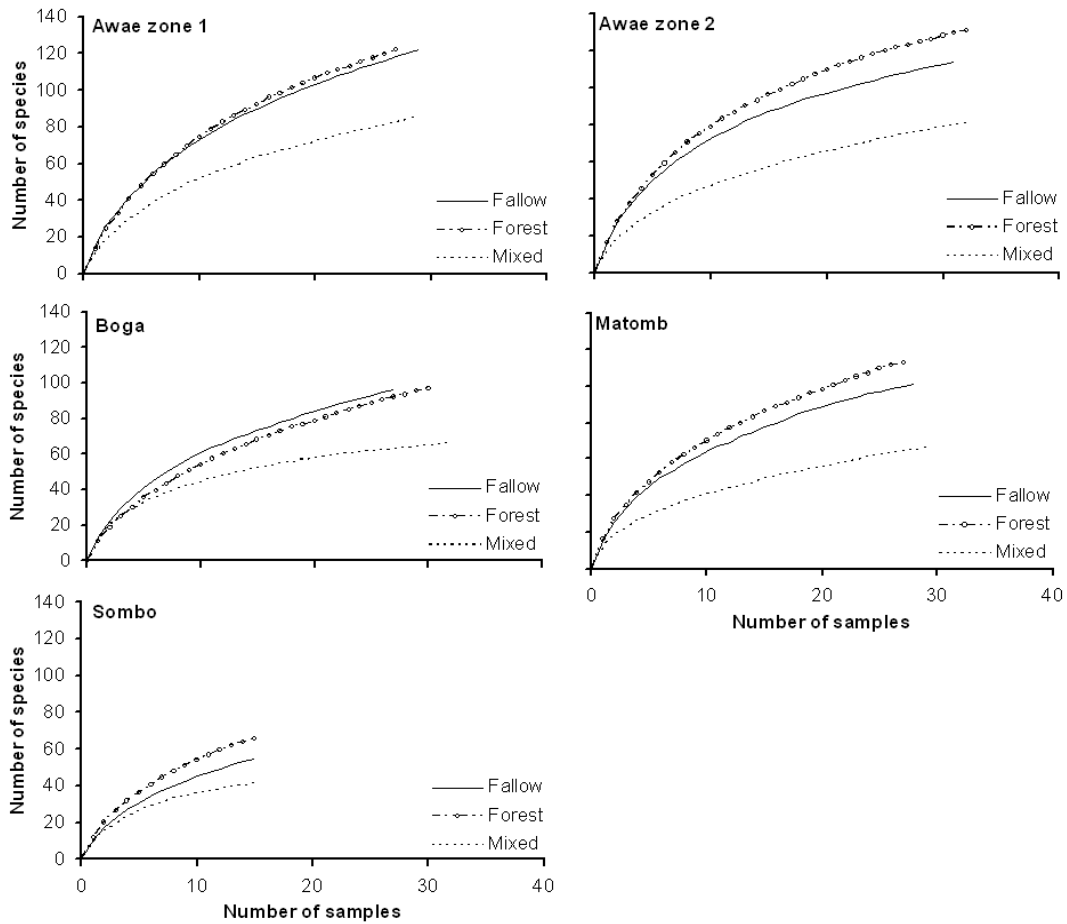
Annex 3: Randomized species saturation curves (2000 runs) of the different plots in each location
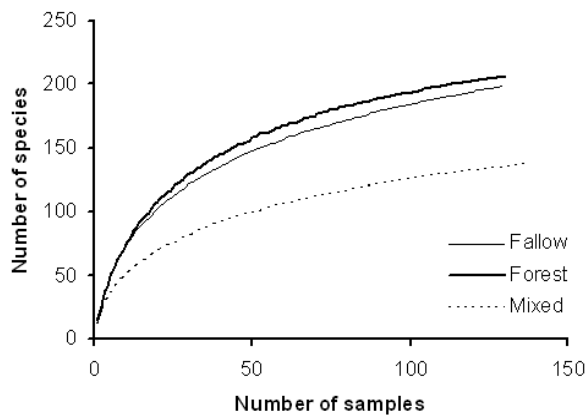
Annex 4: Randomized species saturation curves (2000 runs) of the three vegetation type, all locations pooled together (2000 runs).

134

Annex 5: Measures of species diversity (Number of species Sobs, Shannon-Wiener H', Simpson D, and Evenness J) for the ant communities.

Location	Vegetation	S_{obs}	H'	D	J
	Fallow	125	3.77	20.79	0.78
Awae zone 1	Forest	130	3.85	22.31	0.79
	Mixed	79	3.16	10.62	0.72
	Fallow	113	3.80	22.90	0.80
Awae zone 2	Forest	125	3.79	20.85	0.78
	Mixed	78	3.09	9.48	0.71
	Fallow	98	3.72	24.78	0.81
Boga	Forest	90	3.58	15.18	0.80
	Mixed	65	3.32	18.38	0.80
	Fallow	96	3.57	21.13	0.78
Matomb	Forest	111	3.75	22.09	0.80
	Mixed	66	2.93	11.24	0.70
	Fallow	55	3.28	18.03	0.82
Sombo	Forest	66	3.45	19.16	0.82
	Mixed	41	2.80	8.24	0.75

Annex 6. Mean value of air temperature, air relative humidity and soil temperature in different vegetation type. Comparison between vegetation types was done by one way ANOVA. Tukey's HSD was used as *post-hoc* test and means followed by same letter in each location are not significantly different.

Location	Vegetation type	Air temp.±sd	Soil temp.±sd	RH±sd
	Fallow	21.9±1.1a	23.7±0.7a	84.8±8.5a
Awae zone1	Forest	21.6±1.4b	22.6±0.3b	88.9±9.9b
	Mixed	22.8±1.0c	24.9±1.3c	75.4±9.2c
	Fallow	21.8±1.1a	23.5±0.5a	85.8±11.5a
Awae zone2	Forest	21.9±0.8a	22.6±0.3b	92.9±5.9b
	Mixed	23.3±1.6b	24.8±0.9c	90.3±9.4c
	Fallow	24.7±1.3a	25.4±0.5a	89.3±7.2a
Boga	Forest	23.8±0.9b	24.9±0.8a	95.7±4.9b
	Mixed	25.3±1.3c	26.2±0.8b	81.3±8.7c
	Fallow	22.5±1.2a	23.2±0.5a	91.3±6.9a
Matomb	Forest	22.1±0.9b	22.4±0.3b	94.3±5.2b
	Mixed	23.2±1.2c	24.8±1.0c	82.2±8.6c
	Fallow	26.5±2.0a	25.3±0.4a	76.1±9.9a
Sombo	Forest	25.4±1.3b	24.8±0.1b	85.7±5.7b
	Mixed	26.2±1.3a	25.6±0.2a	82.1±5.0c

136

Annex 7. Mean value of soil characteristics in different vegetation type. Comparison between vegetation types was done by one way ANOVA. Tukey's HSD was used as *post-hoc* test and means followed by same letter in each location are not significantly different.

Location	Vegetation	pH(water)	%Org C	%Total N	C/N	%Org. M
Awae zone1	Fallow	4.4±0.3a	1.1±0.2a	0.1±0.0a	11.1 ±1.4a	2.0±0.4a
	Forest	4.1±0.1b	1.1±0.4a	0.1±0.0a	10.3±0.9a	1.9±0.7a
	Mixed	4.3±0.2ab	0.9±0.1a	0.1±0.0a	10.5±0.7a	1.6±0.2a
Awae zone2	Fallow	4.4±0.1a	1.0±0.1a	0.1±0.0ab	10.5±0.7a	1.6±0.2a
	Forest	4.8±0.3b	1.0±0.2a	0.1±0.0a	10.2±0.9a	1.8±0.3a
	Mixed	4.5±0.2ab	0.9±0.1a	0.1±0.0ab	11.3±1.1a	1.6±0.2a
Boga	Fallow	5.2±0.4a	1.4±0.2a	0.1±0.0a	12.0±0.6a	2.4±0.3a
	Forest	3.9±0.1b	0.9±0.2b	0.1±0.0b	12.0±0.6a	1.6±0.3b
	Mixed	4.7±0.2c	1.1±0.4b	0.1±0.0b	12.6±0.9a	1.9±0.3b
Matomb	Fallow	4.7±0.4a	1.0±0.1a	0.1±0.0a	11.6±1.3a	1.8±0.3a
	Forest	3.9±0.1b	1.4±0.2b	0.1±0.0b	12.4±1.1a	2.3±0.3b
	Mixed	4.5±0.1a	1.0±0.1a	0.1±0.0a	11.2±1.2a	1.7±0.2a
Sombo	Fallow	4.6±0.3a	1.5±0.1a	0.1±0.0a	13.0±1.3a	2.5±0.2a
	Forest	3.9±0.2b	1.3±0.3a	0.1±0.0a	13.6±0.7a	2.3±0.6a
	Mixed	4.8±0.2a	1.4±0.2a	0.1±0.0a	14.1±1.6a	2.4±0.3a

138

CURRICULUM VITAE

APOLLIN FOTSO KUATE

PERSONNAL INFORMATION

Surname: Fotso Kuate
First name: Apollin
Date of Birth: 08 February 1977
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CONTACT INFORMATION

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EDUCATION

- 2007–2010: PhD (SUMMA CUM LAUDE), University of Basel, Switzerland
- 2004: DEA in Animal Biology, University of Yaoundé I, Cameroon
- 2003: Maîtrise in Animal Biology, University of Douala, Cameroon
- 1999: Bachelor of Sciences, University of Douala, Cameroon
- 1996: Baccalauréat, Government High School, Bandjoun, Cameroon
- 1995: Probatoire, Government High School, Bandjoun, Cameroon
- 1992: BEPC, Government High School, Bandjoun, Cameroon
- 1988: CEPE, Catholic Primary School, Kamgo, Bandjoun, Cameroon

DOMAIN OF COMPETENCE

- Insect taxonomy with emphasis on ants
- Insect sampling, rearing, specimen mounting
- Insect-Plants interaction
- Survey of pests and diseases
- Field trials implementation and monitoring
- Data processing

RESPONSIBILITIES

- Team Coordinator, Entomology laboratory, IITA-Cameroon
- Laboratory trials conception and follow-up
- Insect specimen maintenance in the IITA- museum

COMPUTER SKILLS

- Microsoft office 2007 (Word, Excel, PowerPoint, Access)
- SAS software V.9.2
- JMP V6.0
- Estimates V8.00
- Adobe Illustrator

TRAININGS, WORKSHOPS AND SYMPOSIA

- 10-20 July 2010. Training visit at the Institute of Biogeography, University of Basel
- 05-10 July 2010: VIIème Conférence Internationale Francophone d'Entomologie, Louvain-La Neuve, Belgium
- 21-24 April 2009: IITA Partners meeting, Bertoua, Cameroon
- 09-12 June 2008: 8th General Assembly of the West and Central African Council for Agricultural Research and development (WECARD), IRAD, Yaoundé, Cameroon
- 10-20 February 2007. Training visit at the Institute of Biogeography, University of Basel
- 14-16 December 2006:13th Cameroon Biosciences Conference on the theme Biosciences and industrial development, University of Douala
- 6-9 December 2005:1st international symposium on crops integrated pest management in the CEMAC zone, Dschang, Cameroon
- 12-21 July 2004: Training courses in Biometry and computing with SAS version 8, IITA-Cameroon.
- 6-8 October 2003: Workshop on Cassava green mite biocontrol and the development of work plans for the cassava-IPM project, IITA-Cameroon.

PUBLICATIONS AND COMMUNICATIONS

Publications in peer review journals

Akinbade, S., Hanna, R., Nguenkam, A., Njukwe, E., **Fotso Kuate**, **A**., Doumtsop, A., Ngeve, J., Tenku, S.T.N. and Kumar, P.L. 2010. First report of the East African cassava mosaic virus-Uganda (EACMV-UG) infecting cassava (*Manihot esculenta*) in Cameroon. New Disease Reports 21, 22.

Fotso Kuate A., Tindo M., Hanna R., Kenne M. and Goergen G., 2008. Foraging activity and diet of the ant, *Anoplolepis tenella* Santschi (Hymenoptera: Formicidae), in southern Cameroon. African Entomology 16 (1): 107-114.

Publications in preparation

Fotso Kuate A., Hanna R., Tindo M., Goergen G. and Nagel P. Toxicity of Amdro, Borax and Boric acid to *Anoplolepis tenella* Santschi (Hymenoptera: Formicidae). In Prep.

Fotso Kuate A., Nagel P., Tindo M., Goergen G. and Hanna R. Ant diversity in the humid forest zone of Cameroon: Distribution of the pest ant *Anoplolepis tenella* Santschi (Hymenoptera, Formicidae). In Prep.

Fotso Kuate A., Hanna R., Tindo M., Goergen G. and Nagel P. Interaction between ants, plants and honeydew-producers in the humid forest zone of southern Cameroon . In Prep.

Fotso Kuate A., Hanna R., Tindo M., Goergen G. and Nagel P. Transport and dispersal of *Stictococcus vayssierei* (Homoptera, Stictococcidae) by *Anoplolepis tenella* (Hymenoptera, Formicidae). In Prep.

Fotso Kuate A., Hanna R., Tindo M., Goergen G. and Nagel P. Seasonal variation in ant species richness, density and activity in the humid forest zone of southern Cameroon. In Prep.

Publications in proceedings

Fotso Kuate A., Tindo M., Hanna R., Kenne M. and Goergen G., 2006. Field abundance and nest structure of the ant *Anoplolepis tenella* associated with the African root and tuber scale in the Congo Basin. Proceeding of the 1st international symposium on crops integrated pest management in the CEMAC zone, (Eds) Pefoura Mouliom A., Tindo M., Ngoko Z. and Dibog L. Dschang. Pp203-209.

Communications

Fotso Kuate A., Hanna R., Tindo M., Goergen G. and Nagel P. Ant control for the management of the African root and tuber scale: a step forward. **Poster**, International Society for Tropical Root Crops- Africa Branch (ISTRC-AB), Kinshassa, DRC. 4-8 October 2010.

Fotso Kuate A., Hanna R., Tindo M., Goergen G. and Nagel P. Diversité des fourmis dans la zone forestière du sud Cameroun. **Oral presentation**, VIIème Conférence Internationale Francophone d'Entomologie, Louvain-La Neuve, Belgium. 05-10 July 2010.

Fotso Fotso Kuate A., Hanna R., Tindo M., Goergen G. and Nagel P. Ant diversity in the humid forest of Cameroon. **Poster**, CIFOR Forestry day, Yaoundé, Cameroon. 13 November 2009.

Fotso Kuate A., Hanna R., Tindo M., Goergen G. and Nagel P. Control options for the African root and tuber scale on Cassava. **Poster**, 8th general assembly of the West and Central African Council for Agricultural Research and Development (WECARD), IRAD, Yaoundé, Cameroon. 09-12 June 2008.

Fotso Kuate A., Tindo M., Hanna R., Kenne M. & Goergen G. Abondance, structure et composition des nids de la fourmi *Anoplolepis tenella* associée à la cochenille africaine des racines et tubercules dans le basin de Congo. **Poster,** Colloque Annuel de l'Union Internationale pour l'étude des Insectes Sociaux – Section Francaise (UIEIS-SF), Avignon, France. 24-27 Avril 2006.

Fotso Kuate A., Tindo M., Hanna R., Kenne M. and Goergen G. Field abundance and nest structure of the ant *Anoplolepis tenella* associated with the African root and tuber scale in the Congo Basin. Poster, 1st international symposium on crops integrated pest management in the CEMAC zone, 6-9 December 2005.

Thesis

Fotso Kuate A. Towards the development of Sustainable control options for the African root and tuber scale on cassava in Central Africa-understanding the biology and ecology of the tending ant *Anoplolepis tenella* (Hymenoptera; Formicidae). PhD Thesis, Institute of Biogeography, University of Basel, 144 p.

Fotso Kuate A., 2004. Contribution à l'étude de la structure des colonies chez *Anoplolepis tenella* Sanstchi (Formicidae, Formicidae). Master Degree with thesis, University of Yaoundé I, Cameroon, 41p.

Fotso Kuate A., 2003. Eléments de biologie de *Anoplolepis tenella* (Formicidae, Formicidae) associée à la cochenille Africaine des racines et tubercules, *Stictococcus vayssierei* (Homoptera, Stictoccocidae). Masters'thesis, University of Douala, Cameroon, 45 p.

LANGUAGE

Languages	Read	Write	Speak
French	Excellent	Excellent	Excellent
English	Very good	Very Good	Good
Ghomala'(native)	Excellent	Excellent	Excellent

PERSONAL INTEREST

- African traditional dances
- Poetry and songs (St Augustin Choir, Central Africa Catholic University, Yaoundé)
- Cinema, theatre
- Cooking

144