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The effect of ground vegetation management on competition between the ants *Oecophylla longinoda* and *Pheidole megacephala* and implications for conservation biological control

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A B S T R A C T

In tropical Africa and Asia, two species of the predatory ant genus, *Oecophylla*, play a crucial role in protecting tree crops against pests and enhancing the quality of fruits and nuts. As predatory effectiveness is influenced by the presence of other dominant ant species, understanding the ecological factors at work in agroecosystems lies at the basis of conservation biological control. Over three and a half years, the effect of ground vegetation management on the beneficial tree-nesting ant *Oecophylla longinoda* (Latreille) and its competitor, the ground-nesting ant, *Pheidole megacephala* (Fabricius), was studied in a citrus orchard in Tanzania. When ground vegetation was present, *P. megacephala* tolerated *O. longinoda* and to some extent cohabited with this ant in citrus trees. However, after clean cultivation, *P. megacephala* displaced *O. longinoda* from tree crowns and became the sole occupant of the majority of trees. Displacement could be reversed by reversing the weed management regime, but this took time. Two years after the establishment of ground vegetation about half of the trees were colonized by *Oecophylla* only. Maintaining ground vegetation in tree crop plantations benefits the establishment and abundance of *Oecophylla* over *Pheidole* and is recommended in order to improve the efficiency of biological control of tree pests. The use of Amdro ant bait (hydramethylnon) to control *P. megacephala* is discussed. Boosting agroecological innovations, such as the one described in this paper, could benefit smallholder producers.

1. Introduction

Agroecosystems carry a range of ant species, many of which may be cryptic. The species that have received most attention are those known to be either economic or domestic pests, beneficials or both. The ant species that is numerically predominant in any area is considered dominant, and determines pest distributions. Certain dominants are able to co-exist and are referred to as co-dominants, whereas other dominant ants may compete for resources, such as nesting sites and food, and displace one another locally (Majer, 1972).

The primarily ground-nesting big-headed ant, *Pheidole megacephala* (Fabricius), occurs throughout the tropics and subtropics. It preys on a wide range of pests and collects nectar, pollen and small seeds from the ground surface (Perfecto and Castiñeiras, 1998). Farmers in Cuba protect and deploy *P. megacephala* as it prevents weevils from laying eggs on subterranean parts of sweet potato and banana plants. In coffee and pineapple this ant is considered a pest because it protects mealy bugs that transmit viral diseases.

The arboreal weaver ants *Oecophylla longinoda* (Latreille) and *Oecophylla smaragdina* (Fabricius) are two of the most effective species in controlling a wide range of tree pests in Africa, Asia and Australia (Van Mele, 2008a). However, ecologically dominant ground-nesting species can compete with dominant arboreal species to occupy tree crowns more readily in orchards than in rain forests because of the lower canopy in orchards (Kenne et al., 2003). *P. megacephala* is considered to be the most efficient and most widely distributed competitor of *O. longinoda* (Perfecto and Castiñeiras, 1998). When *Oecophylla* faces strong competition, it defends its territory, and consequently its effectiveness to control tree pests is reduced. In order to establish thriving colonies of *Oecophylla*, other dominant ants present may require management. Knowledge of which plants favour which competing ant species is important when designing agroecosystems (Van Mele and Chien, 2004; Van Mele, 2008b).

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Traditional citrus farmers in Vietnam have developed a good knowledge of the relationship between *O. smaragdina*, the main tree crop and accompanying crop and non-crop plants (Van Mele and Cuc, 2000). In East Africa, smallholder farmers typically interplant coconut palms with a wide variety of food and cash crops. Although most African farmers were initially not aware of the underlying ecological mechanisms, the practice of citrus intercropping enhances coconut production because it supports the beneficial ant *O. longinoda* that controls fairly effectively the coconut bug *Pseudotheraptus wayi* Brown (Seguni, 1997). Most tree crop owners and coconut climbers in Tanzania appreciate the benefits of *Oecophylla* to such an extent that they have developed multiple creative ways to reduce its nuisance (Van Mele et al., 2009). Basic food crops such as cassava, maize, pulses and sweet potatoes comprise a large part of this intercropping complex. The cash crops used include fruits, notably pineapple, banana and plantain and trees such as citrus, mango, members of the family Annonaceae, guava, and cashew. On the islands of Zanzibar and Pemba, cloves and cinnamon are also widely cultivated intercrops that favour *O. longinoda* establishment (Varela, 1992; Way, 1953).

Little information is available on the effects of ground vegetation on ant competition and displacement. In Tanzania, coconut groves intercropped with arable crops are usually clean cultivated, whereas those interplanted with tree crops may have ground vegetation, which is periodically slashed or grazed by cattle. Way (1953) noted that in Zanzibar, *O. longinoda* was more successful in environments where bush and certain tree crops, notably citrus, mango, and clove, were growing together with coconuts, whereas the more arable areas were largely populated by its competitor ant, *P. megacephala*. These observations indicate that the ground vegetation and shrubs are likely to affect ant interactions. Way (1953) suggested manipulating vegetation in coconut fields in order to favour the more beneficial weaver ant. In the Solomon Islands, O'Connor (1950) suggested that improved coconut protection from the coreid bug, *Amblypelta cocophaga* China, during the post-war years, was due to increased colonization of coconut palms by *O. smaragdina* following neglect of the plantations, which had become overgrown. He therefore advised encouraging vegetation, especially creepers, which could provide trails between trees. However, the "creeper theory" was refuted by Brown (1959), who could not find any correlation between increases of *O. smaragdina* and creeper vegetation. Rapp and Salum (1995) reported that when weeds died in coconut plantations, *P. megacephala* was often observed raiding *Oecophylla* nests in coconut palms.

Interactions between weeds and pest and beneficial arthropod populations have recently been reviewed in the light of conservation biological control (Landis et al., 2000; Norris and Kogan, 2005, Jonsson et al., 2008), but the bulk of examples cover annual cropping systems in temperate zones. Most ecological studies on weed/ant interactions in tropical tree crop plantations are descriptive in nature and no long-term habitat manipulation experiments have been published that measure displacement dynamics of the competing ants, *P. megacephala* and *O. longinoda*. To address this, we examined the effect of different ground vegetation management regimes in a citrus orchard on the interrelationship between *P. megacephala* and *O. longinoda* over a three and a half-year period.

2. Methods

The experiment was conducted in a uniform citrus orchard of approximately 2 ha at Mwanambaya village, about 35 km south of Dar es Salaam, Tanzania. The trial area had a bimodal rainfall pattern with average annual precipitation ranging between 1100 and 1300 mm. The short rainy season occurs from October to December, while the long rainy season lasts from the end of March to June. It is hot (27–30 °C) and humid year-round with a relatively cool season from June to September when temperatures drop slightly to 25–28 °C. The main species were *Panicum trichocladum* K. Schum., *Cynodon dactylon* (L.) Pers, *Bidens* spp. and *Comellina* spp. The *Pheidole* ants attended aerial scales on the grasses and herbaceous vegetation, of which the latter probably also provided nectar. Before the start of the experiment, the ground vegetation had already been cleared in half of the orchard, whereas ground vegetation had been retained in the other half.

Grafted orange trees of 3.3–4 m in height were grown 7 m apart in rows with 9 m in between rows. The trees harboured various homopterans, such as aphids and scales. One half of the orchard was clean cultivated by hoeing at three-month intervals, whereas in the other half weeds were maintained but kept low to about 10 cm by hand slashing at similar intervals. From December 1992 to June 1996, at three-monthly intervals, colonization of tree canopies by the co-dominants was assessed in two blocks of 10 × 10 trees, one in each half of the orchard. Each block was surrounded by about five rows of citrus trees, which acted as guard rows. In order to confirm the impact of ground vegetation management on *P. megacephala* and *O. longinoda*, the treatments were reversed after two years. In March 1994 the previously clean weeded block was left to re-develop ground vegetation, and the weeds in the block with ground vegetation were regularly removed.

The presence and abundance of the two ants were recorded on all trees of each block. One experienced person counted *P. megacephala* while another person counted *O. longinoda*. The presence and abundance of *P. megacephala* were recorded during a five minute inspection per tree, using six classes whereby: 0 meant that no ants were observed; 1 = 1–20 ants were observed (average = 10.5); 2 = 21–50 (35.5); 3 = 51–100 (75.5); 4 = 101–200 (150.5) and 5 = 201–500 (350.5) ants. For *O. longinoda*, active nests with foraging workers were counted and classes of worker ants assessed foraging on the main branches. During a five minute inspection the classes were assessed as follows: 0 = no ants seen; 1 = 1–5 ants seen (average = 3); 2 = 6–10 (8); 3 = 11–20 (15.5); 4 = 21–50 (35.5) and 5 = 51–100 (75.5) ants. We did not use a ladder because the tree canopies were easily observable. In the analysis, the averages for each class were used and average data were calculated for specific times before and after the weed management regime was reversed in each block. Data were analyzed using Student's *t*-test. Maps were used to visualize shifts in colonization by *P. megacephala* and *O. longinoda* of each tree in each block at the beginning, middle and end of the experiment.

3. Results

3.1. Overall distribution of ants before and after reversing weed management regime

Figs. 1–3 show the distribution of *P. megacephala* and *O. longinoda* at the start of the observation in December 1992, in March 1994 soon after reversing the cultural practices and in June 1996 at the end of the observations. In the clean cultivated plot in December 1992, *P. megacephala* was present on all the citrus trees either at the bases but also foraging in the tree crowns. *O. longinoda* occupied only 3% of the trees at the boundary with the weedy plot. Nearly all trees had many *P. megacephala* at their bases. In the plot with ground vegetation, *P. megacephala* was the sole occupant of only 19% of the citrus trees. The remaining 81% of the trees were occupied by both *P. megacephala* and *O. longinoda*, either with *P. megacephala* confined to the bases of the trees or also sharing the tree crowns with *O. longinoda* (Fig. 1). In March 1994, nearly 15 months after starting the observations and soon after the reversal of the weed management regime, the status of

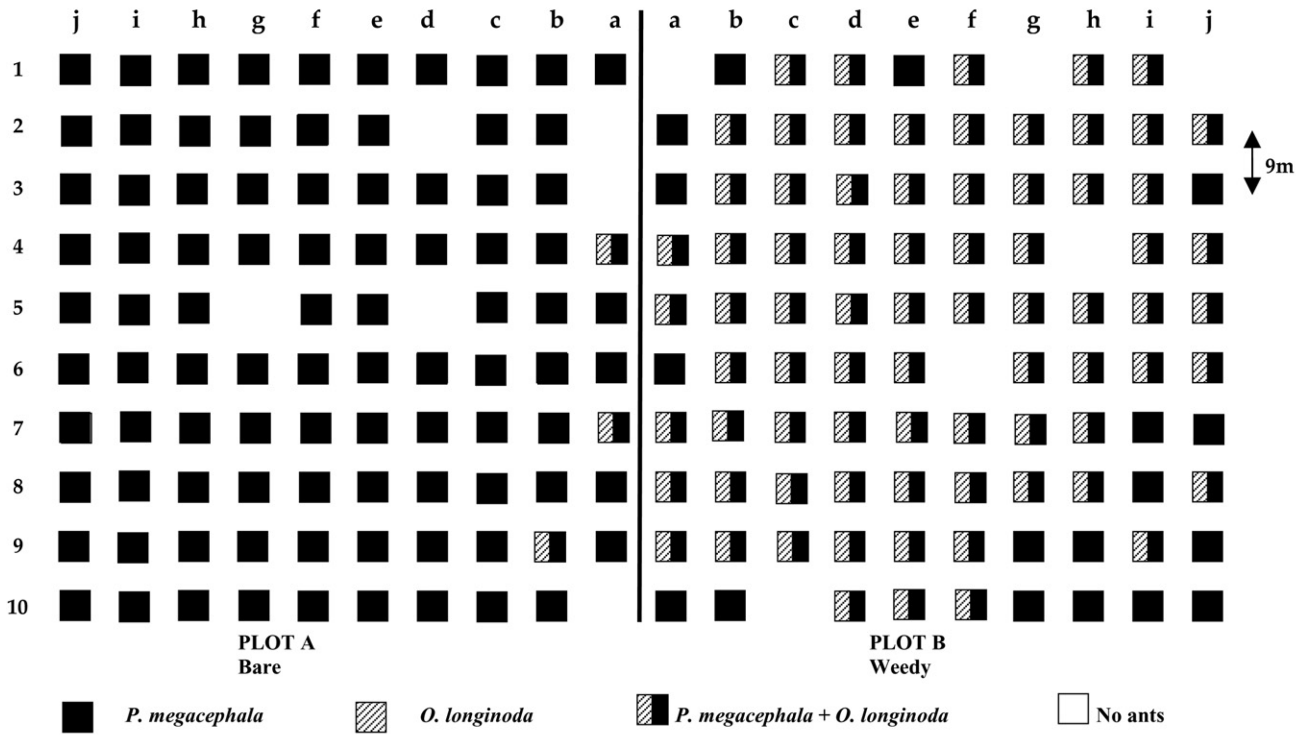

Fig. 1. Distribution of *Oecophylla longinoda* and *Pheidole megacephala* on citrus in plots with and without ground vegetation in December 1992. Open boxes indicate missing trees.

P. megacephala and *O. longinoda* in the clean cultivated plot remained basically unchanged (Fig. 2). *O. longinoda* was in 6% of the trees while *P. megacephala* continued to occupy all trees in the plot. Soon after clean weeding the weedy plot, *P. megacephala* and *O. longinoda* continued to occur on 62% of the trees together, while *P. megacephala* and *O. longinoda* had become sole occupants on 33% and 4% of trees respectively, and on 1% of trees neither ant was observed.

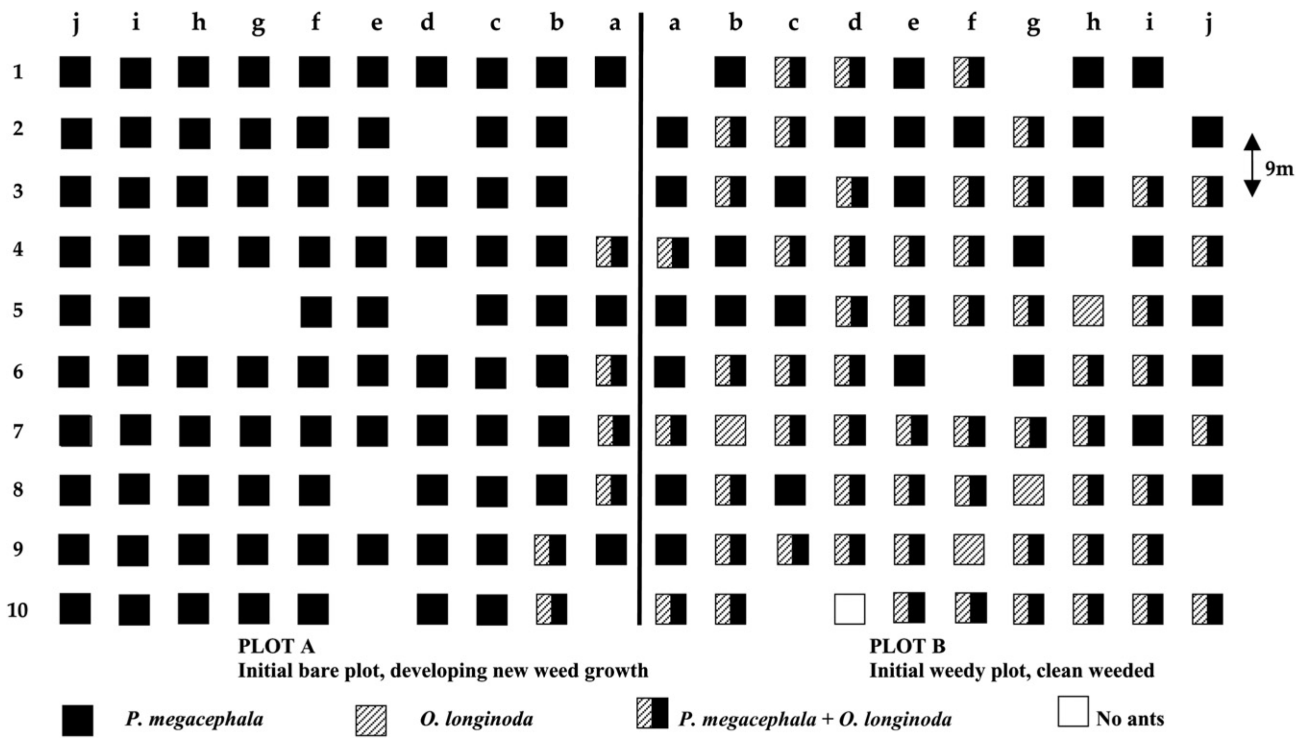

Fig. 2. Distribution of *Oecophylla longinoda* and *Pheidole megacephala* on citrus in newly bare and weedy plots of citrus soon after reversing weed management regime in March 1994. Open boxes indicate missing trees.

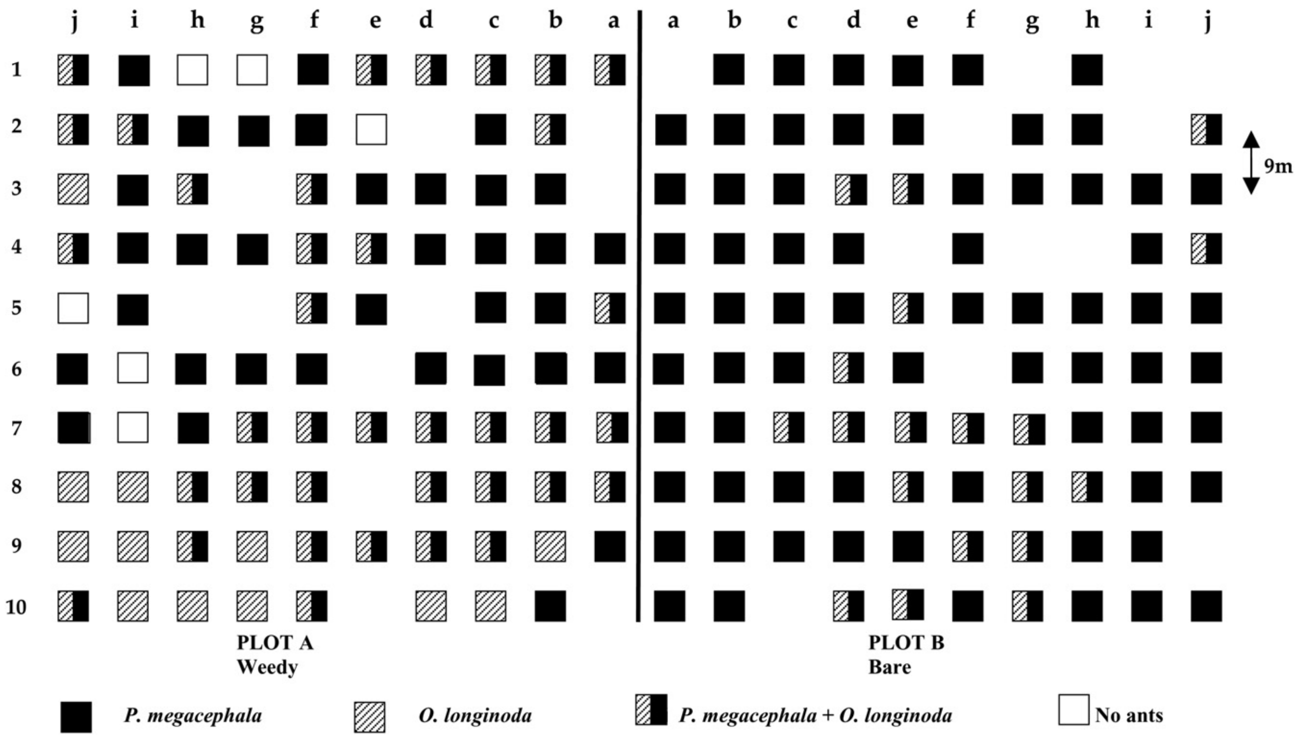

Fig. 3. Distribution of *Oecophylla longinoda* and *Pheidole megacephala* on citrus 29 months after reversing weed management regime in June 1996. Open boxes indicate missing trees.

Twenty seven months after the reversal of weed management the species distributions are largely reversed also (Fig. 3). On the initially bare plot, after grasses and herbs covered the ground and were about 10 cm high, tree occupancy by *O. longinoda* had increased to 55% with 76% of trees being shared by the two ants, while 24% had *O. longinoda* as sole occupant. *P. megacephala* was the sole occupant of only 38% of trees while 7% of the trees had neither ant. On the original weedy but now bare plot the number of trees with *O. longinoda* had declined from 81% to 22% whereas trees that were solely occupied by *P. megacephala* had increased from 32% to 78%.

3.2. Overall number of ants before and after reversing weed management regime

The average number of individual *P. megacephala* per tree base on the initially weedy plot decreased soon after clean weeding started but over the two years of clean cultivation their numbers increased significantly ($P < 0.05$). A similar trend was observed at the initially bare plot, although here the numbers increased to about the pre-reversal levels when ground vegetation was fully established (Table 1). *P. megacephala* tendency to occupy tree crowns increased in the absence of ground vegetation, while canopy colonization by *O. longinoda* followed the opposite trend. The number of *O. longinoda* ants and leaf nests per tree increased significantly ($P < 0.05$) when ground vegetation was allowed to develop.

4. Discussion

Vanderplank (1960), working in Zanzibar, reported that *Oecophylla* and *Pheidole* sp. do not actually overlap spatially in coconut plantations. In a world-wide study of nesting ant communities in coconut palms, Way and Bolton (1997) showed that *P. megacephala* was absent or relatively scarce where *O. longinoda* was abundant. Under environmental stress conditions, such as at times when soils were waterlogged, *Pheidole* sp. moved up the tree trunks and suppressed both *O. longinoda* and other tree-nesting ants, suggesting intolerance in foraging areas. Other dominant ant species such as the little fire ant, *Wasmannia auropunctata* (Roger), and the

Table 1
Changes in presence of the co-dominant ants *P. megacephala* and *O. longinoda* in two citrus plots with different undergrowth and weed management regimes (number of trees sampled = 89–94). Treatments were reversed in March 1994.

Condition of undergrowth	*Pheidole megacephala*			*Oecophylla longinoda*		
	Percentage of tree bases occupied	Mean no. at base/tree	Percentage of tree crowns occupied	Percentage of tree crowns occupied	Mean no. of ants/tree	Mean no. of nests/tree
Ground vegetation present (Dec 1992)	99	207[a]	19	81	36[a]	5.2[a]
Initial stage of bare soil (May 1994)	52	159[b]	54	85	20[ab]	2.7[b]
Established bare soil (June 1996)	93	273[c]	78	20	16[b]	2.9[b]
Bare soil (Dec 1992)	100	250[a]	97	3	1[a]	0.2[a]
Initial stage of ground vegetation (May 1994)	83	158[b]	68	6	5[a]	1.2[b]
Ground vegetation fully developed (June 1996)	91	273[a]	38	53	21[b]	2.8[c]

[a,b,c] Means in columns within each experimental block followed by a different letter are significantly different at 0.05 level (Student's *t*-test).

large ponerine, *Odontomachus bauri* Emery, seemed mutually tolerant, but much depended on the abundance levels of each individual species. The authors concluded that "apparently simple dominance and displacement concepts can be relatively complex when applied to competition for similar nesting sites, and that this needs to be taken into account in the use of beneficial ants that are important in biological control, and in the suppression of their harmful competitors."

Although our experiments were not set up to analyse causation, we show that in citrus, co-existence of *O. longinoda* and *P. megacephala* is possible, and that tolerance levels are influenced by the weedy undergrowth. When bare soil conditions were present, *P. megacephala* foraged in the tree crowns to the detriment of *O. longinoda* populations. However, two years after allowing weeds to grow to some extent, *P. megacephala* numbers in tree canopies decreased and *O. longinoda* colonized a larger number of trees, implying that co-existence of the primarily ground-nesting *P. megacephala* with the tree-nesting *O. longinoda* is a dynamic process, influenced by the ground cover.

Prior to the removal of ground vegetation there seemed to be greater tolerance between the two ants, although competition no doubt occurred. The initial decrease in *P. megacephala* after removal of vegetation may have been due to sudden hostile bare soil conditions, such as reduction of suitable nesting sites and food supply. The initial effect of creating bare soil conditions on *P. megacephala* was similar to that observed in the Solomon Islands, where clean cultivation was recommended as a possible method for controlling *P. megacephala*, as this ant is susceptible to desiccation (Greenslade, 1971). However, our experiments showed that *P. megacephala* is only temporarily reduced by clean cultivation and recovers after initial disturbance. As clean cultivation resulted in more *P. megacephala* in tree canopies this reduced numbers of *O. longinoda* and presumably its effectiveness as a biological control agent. *P. megacephala* regained high abundance levels on the ground between tree rows in the newly established bare soil conditions. Combined with their efficient recruiting system and aggressiveness towards other ant species, the highly efficient predatory capacities of *P. megacephala* help explain its ecological success (Dejean et al., 2007).

As some intercropped plants affect interrelationships between dominant ant species, a key to developing sustainable tree cropping systems is to understand the factors that shape such interactions (Van Mele and Chien, 2004). We show here that occasional hand slashing of the weedy undergrowth is more beneficial than clean cultivation in promoting effective conservation biological control with the weaver ant *O. longinoda*. Probably, clean cultivation affected the *Pheidole* nesting sites in the soil by exposing them to intense sunlight. Also, the removal of weeds harbouring honeydew-producing homopterans turned the citrus trees into the only source of honeydew.

Other interventions may be needed to control competiting ants to the benefit of *Oecophylla*. One possibility could be to adopt Amdro ant bait (hydramethylnon), which has been used extensively in pineapple (see for instance Taniguchi et al., 2005) and also in mature coffee orchards where it controlled *P. megacephala* to a significant extent within 3 months and brought total control in 8 months (Arakaki et al., 2009). Considering the time needed for arboreal ants to re-establish themselves after having been displaced by other dominants (this paper), or after trees have been sprayed with insecticides (Kenne et al., 2003), the use of Amdro might increase the rate of (re)colonization by *Oecophylla*.

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