Interference Between Ant Species Distribution in Different Habitats and the Density of a Maize Pest

by

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ABSTRACT

A field study conducted on maize plants growing in three different conditions (one or two rows cultivated along the walls of houses in working-class districts of Yaoundé, Cameroon; vacant lots of the city that we call «urban gardens»; and an experimental field outside the city) revealed that the plants were attacked by the corn delphacid, *Peregrinus maidis* (Ashmed) (Homoptera; Delphacidae), a vector of maize viral diseases. Damages were significantly greater (1) along the walls than in the urban gardens; (2) in the urban gardens than at the edges of the field; and (3) at the edges than in the center of the field. The number of *P. maidis* individuals per plant was greater on maize plants growing along the walls than in the urban gardens, while we did not record differences between the latter and those situated along the field edges or between edge and center of the fields. We recorded a significant correlation between ants and *P. maidis* presence on maize plants. Destruction of ant nests by ploughing resulted in less ants foraging on maize and consequently fewer plants attacked by *P. maidis*. Ant species compete to attend *P. maidis*, although attendance is influenced by varying ant distribution patterns under the three growing conditions. The number of *P. maidis* individuals per maize plant varies as a function of the attending ant species. Comparison with controls where ants were excluded indicated no differences in levels of *P. maidis* when attended by *Paratrechina longicornis* (Latreille), while other comparisons with the controls resulted in significant differences. The number of *P. maidis* individuals per maize plant was significantly higher when attended by *Camponotus acvapimensis* (Mayr) than by *Crematogaster* sp. or *Pheidole*

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megacephala (F.) and was also higher when attended by both of the latter than by *Myrmicaria opaciventris* (Emery). We therefore advise (1) to avoid growing maize along the walls of houses in the cities, (2) to destroy ant nests situated in and around the urban gardens, and (3) to plough prior to planting maize over a large zone around the fields.

Key words: ant distribution, trophobiosis, *Peregrinus maidis*, Homoptera, Delphacidae, pest control

INTRODUCTION

Both in nature and agriculture, ant-homoptera associations can indirectly benefit their host plants through protection against herbivory (Messina 1981; Beattie 1985; Perfecto 1990). Nevertheless, in agriculture these associations frequently result in a proliferation of homopterans, resulting in increase of damage to the host plant (Samways 1990; Way & Khoo 1992; Dejean & Matile-Ferrero 1996). Moreover, certain homopterans are vectors of plant diseases, as is the case for the corn delphacid, *Peregrinus maidis* (Ashmed) (Fulgoromorpha, Delphacidae), the only known vector of two widely distributed viral diseases of maize (maize mosaic virus and maize stripe virus) and of nonspecific maize viruses (Conti 1985; Nault 1987).

As a consequence of economic hardship every open lot in Yaoundé (Cameroon) has been planted with maize. In May 1992, we observed that numerous maize plants were heavily attacked by *P. maidis* and we noted the presence of ants. We first studied the trophobiotic associations between *P. maidis* and ants and then the influence of tramp ant species on the proliferation of this pest (Dejean *et al.* 1996, 1997).

In this study, we formulated the following hypotheses, namely.

(1) Ant nest destruction by agriculture may have repercussions on the degree of maize plants attack by the pest. To investigate this we compared three growing conditions: maize plants growing along the walls of houses in the city (ant nests preserved as situated at the bases of the walls); small urban gardens (ploughing by hand destroyed ant nests, but ants from the unploughed areas adjacent to gardens had access to all the maize plants); a field (deep ploughing destroying nests; the center is far from the edges) permitting us to test if there is a field edge effect.

(2) Ant species may compete to attend *P. maidis* and influence its abundance. We compared ant species distribution (attracted by baits) versus association with *P. maidis* on maize plants in the three different conditions, and the number of pest individuals per maize plant as a function of the attending ant species.

MATERIALS AND METHODS

This study was undertaken in June and July 1992 and 1993, a period just preceding the harvesting of maize in the Yaoundé region. We compared three growing conditions: (1) maize plants cultivated along the walls of houses of working-class districts (one or two rows of maize plants; ant nests situated at the bases of the walls not disturbed), (2) small vacant lots of the city called «urban gardens» (ant nests destroyed; but the center was close to the edges), and (3) an experimental field of the Institute of Agronomic Research (IRA), situated 8km from the center of the city (ant nests destroyed; the center was far from the edges). The same variety of maize was grown in the three cases.

In order to know the ant species distribution in the different conditions, we distributed baits (three drops of honey deposited on a 7.5 x 7.5cm sheet of paper fixed to the soil by a small stake): between the house wall and the first row of maize (approximately every 70cm; 170 baits); every meter over four rows chosen at random in the urban garden; and in the center of the field of the IRA (19 x 20m) (80 baits in each case); and every 3m between the first and the second rows around the field (100 baits). Attracted ants were collected 20 minutes after the baits were deposited. Ants were identified on site and voucher specimens were sent to the Museum of Natural History, London.

Some 786 maize plants were sampled by selecting: (1) 460 maize plants along the walls of houses; (2) 167 maize plants in urban gardens (one plant out of five in a garden of 20 x 17m; and 10 plants chosen at random in each of five others); (3) 106 plants at the periphery and 53 plants in the center of the field of the IRA (100 x 55m; one plant out of five). We noted for each maize plant sampled the presence versus absence of *P. maidis* and, when present, the ant species attending it.

We counted *P. maidis* individuals per maize plant early in the morning, by cautiously opening the bases of the leaves where they shelter. When numerous, they were captured with an aspirator and then counted in the laboratory. This was done for 230 maize plants from three plantings along the walls in the city, 84 in an urban garden, plus 33 from the periphery, and 42 from the center of the field of the IRA. The effect of the ant species on the pest was controlled in 1993 by excluding ants from 20 maize plants in an urban garden. We brushed over the bases of the plants with birdlime each week, permitting us to compare these control plants with 69 others.

Statistical comparisons were made using Wilcoxon matched-pairs test (Statistica 5.1 software). For multiple comparisons we used the Fisher's exact-test (StatXact 2.05 software), and appropriate probabilities were adjusted for the number of simultaneous tests, using the sequential Bonferroni procedure (Rice, 1989): at the significance level (α=0.001 or 0.05), statistical probabilities "P" were determined for "k" total number of pairwise tests and were ranked from smallest (P_1) to largest (P_k). For independent samples (our situation), the test corresponding to P_i indicated significance if $P_i \leq (1-[1-\alpha]^{1/(1+k-i)})$.

RESULTS AND DISCUSSION

Influence of ant activity on P. maidis under different growing conditions

The frequency at which maize plants were attacked by *P. maidis* was significantly greater on plants growing along the walls in the city than those in the urban gardens; in the urban gardens than in the first row of the field; and in the first row than in the center of the field (Fig. 1). The number of *P. maidis* individuals attacking maize plants cultivated along the walls in the city was higher than those of urban gardens (mean

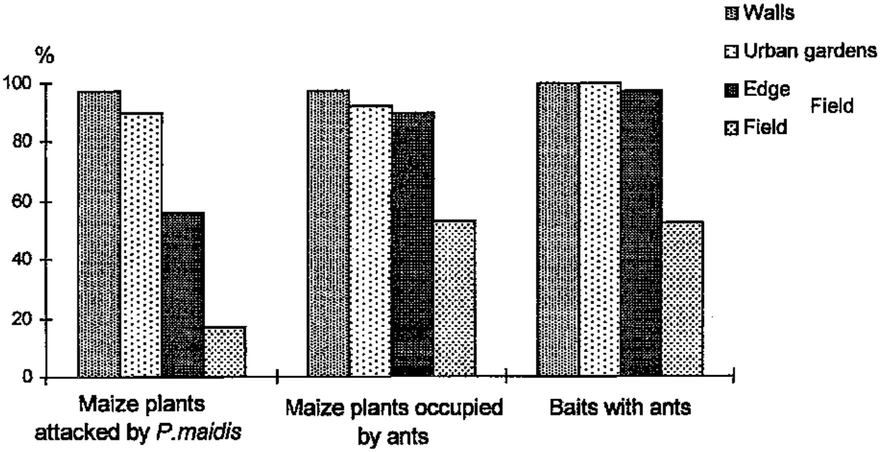

Fig. 1. Influence of the growing conditions on the percentage: (1) of maize plants (N=786) attacked by *P. maidis*; (2) of maize plants foraged by ants; and (3) of baits (N=430) discovered by ants in 20 minutes. Statistical comparisons between different growing conditions (four cases among the six permutations possible) (Fisher exact test and sequential Bonferroni procedure: ** for p<α', with α' corresponding to the significance level α=0.001; * the same with α" corresponding to α=0.05):

	Walls *vs.* urban gardens	Walls *vs.* edge of the field	Urban gard. *vs.* edge of the field	Edge *vs.* center of the field
P. maidis	p=0.0006 α'=0.001**	p=1 x 10^{-25} α'=0.0002**	p=2 x 10^{-10} α'=0.0003**	p=8 x 10^{-7} α'=0.0005**
Ants/maize	p=0.0075 α"=0.025*	p=0.0026 α"=0.017*	p=0.66 NS	p=8 x 10^{-14} α'=0.0002**
Ants/baits	100% baits occupied by ants in both situations**	NS	NS	α'=0.0002 **

±SE; Wilcoxon matched-pairs test; 382.8±47.6; N=84 *vs.* 103.03±13.3; N=30; T=94; p=0.004) or the first row of the field (122.9±15.3; N=33; T=1445; p=2 x 10^{-6}), while the difference between the two latter cases was not significant (T=114; p=0.11).

It appears therefore that the growing conditions influence both the rate of maize plants attacked by *P. maidis* and the number of pest individuals per maize plant. These differences may depend: (1) on the growing conditions of the plant which may favor the pest directly or indirectly if the density of its enemies, such as parasitoids, is low; and/ or (2) indirectly on the influence of ant activity on *P. maidis*.

The percentage of maize plants foraged by ants did not follow exactly the same pattern as that of attacks by *P. maidis* (significant differences between walls and urban gardens, walls and the edge of the plantation, the edge and center of the plantation as for *P. maidis* but no significant difference between urban gardens and the edge of the field), providing arguments in favor of a combination of both above-cited effects (Fig. 1).

Therefore, ant activity is a very important parameter influencing variations registered in the percentage of maize plants attacked by the pest. For example, we recorded in all cases a significant positive correlation between the presence of *P. maidis* and the presence of ants on the maize plants (Fig. 2).

Influence of the growing conditions on ants and on the rate of maize plants attacked by *P. maidis*

The first indications of the influence of growing conditions on workers' foraging were provided when we noted that ants occupied significantly fewer baits in the center of the field than in the three other growing conditions (which were occupied similarly) (Fig. 1).

It could be that ant nest destruction by agriculture results in a decrease in the rate of maize plants attacked by the pest. This was certainly possible as we recorded more maize plants with both ants and *P. maidis* present (1) along the walls in the city than in the urban gardens, (2) in the urban gardens than at the edges of the field, and (3) at the edges than in the center of the field (Fig. 2).

We noted that the destruction of the ant nests was almost null in the first case, as the nests were preserved by being situated at the bases of the walls; high in the urban gardens due to earth being ploughed by hand (only a few nests survived, but the effect was superficial); and very strong in the field due to the use of machinery (the earth was ploughed deeply, including a 2m zone surrounding the maize). As a result, the nests of all ant species were destroyed. In the field, ant presence and activity on maize plants decreased from the edge to the center (field edge

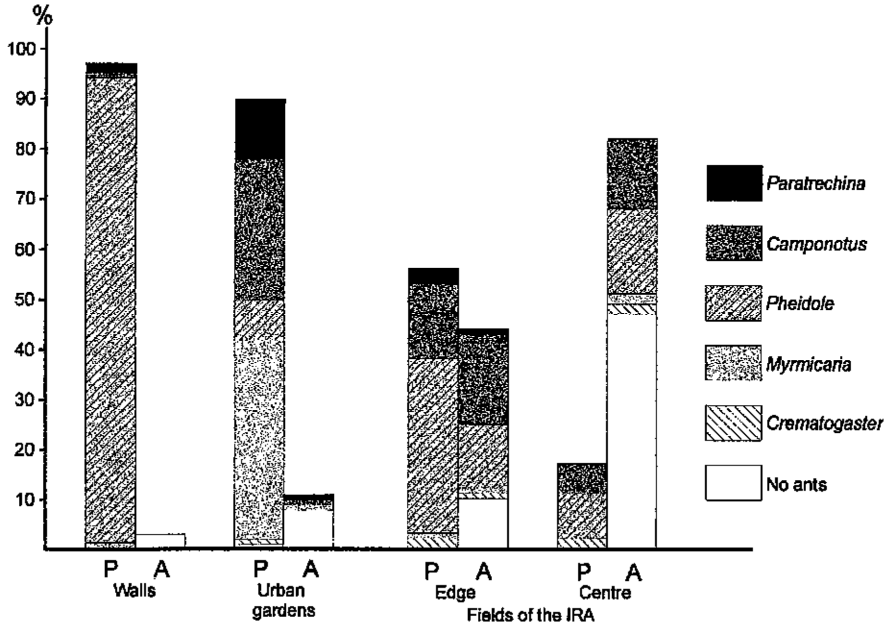

Fig. 2. Comparison of presence (P) versus absence (A) of *P. maidis* on maize plants in different growing conditions, with reference to ant species recorded on these plants (786 maize plants analyzed). There is a significant positive correlation between the presence of *P. maidis* and the presence of ants (point-tetrachoric coefficient of correlation between two binary variables; r_f and the Fisher exact test): walls of the houses: r_f=+1; N=460; p=5 x 10^{-27}; urban gardens: r_f=+0.832; N=167; p=9 x 10^{-16}; periphery of the fields: r_f=+0.381; N=106; p=6 x 10^{-5}; center of the fields: r_f=+0.427; N=53; p=0.002) (walls: N=430; urban gardens: N=167; field edges: N=106; field center: N=53). Comparisons between the different milieu (Fisher exact test and sequential Bonferroni procedure: ** for p < α', with α' corresponding to the significance level α=0.001; * the same with α" corresponding to α=0.05.):

	Walls *vs.* urban gardens	Urban gard. *vs.* edge of the field	Edge *vs.* center of the field
Both ants and	p=0.0001	p=1 x 10^{-10}	p=8 x 10^{-7}
P. maidis present	α'=0.001 **	α'=0.0003 **	α'=0.0005 **
Ants and	p=0.0075	p=0.66	p=8 x 10^{-14}
P. maidis absent	α"=0.0025 *	NS	α'=0.0002 **

effect).

The system of tunnels connecting the nests of *Myrmicaria opaciventris* (Emery) (see Suzzoni *et al.* 1994; Kenne & Dejean 1999) situated in unploughed areas of the urban gardens was preserved as it was deep enough, but not in the fields.

The observed field edge effect can be compared to the results of Orlob (1963), Breadsley *et al.* (1982) and Jahn & Breadsley (1994). The first case concerns ant-attended aphid colonies on maize, while the others concern ant-attended Pseudococcidae (principally by *Pheidole* *megacephala* [F.]) on pineapple (note that in the three situations the homoptera transmitted plant diseases).

Ant species associated with *P. maidis*

We noted the presence of only one ant species per bait or maize plant. Among the 21 ant species attracted by baits, 14 from the subfamilies Myrmicinae, Dolichoderinae and Formicinae were recorded as attending *P. maidis* on the maize plants (Table 1). Four ant species (*M. opaciventris*, *Ph. megacephala*, *Camponotus acvapimensis* [Mayr] and *Paratrechina longicornis* [Latreille]) dominated both on the baits and on the maize plants, with *Ph. megacephala* being the most frequent.

Table 1. Distribution of ant species on baits and on maize plants attacked (P) or not (A) by *P. maidis* (* arboreal nesting ant species).

	CITY						FIELD					
	Rows along the walls			Urban gardens			Periphery			Center		
P. maidis: present / absent	Baits	P	A	Baits	P	A	Baits	P	A	Baits	P	A
PONERINAE												
Odontomachus troglodytes				1								
MYRMICINAE												
Atopomyrmex mocquerisii *							1					
Crematogaster clariventris *				1	1		1	2				
Crematogaster castanea *				3	1		1					
Crematogaster spp. *									1	1	1	1
Crematogaster striatula							12					
Monomorium sp.							2			1		
Myrmicaria opaciventris	9	2		28	66		16	1	1	7		1
Pheidole megacephala	54	430		19	13	1	13	36	14	9	5	8
Pheidole spp.					1		6	1		4		1
Tetramorium spp.							2			1		
DOLICHODERINAE												
Tapinoma melanocephala	33			2								
Tapinoma sp.							2					
FORMICINAE												
Anoplolepis tenella							11			1		
Camponotus acvapimensis				1	7		15	15	17	14	2	5
Camponotus brutus		6			8	1	2	1		1	1	1
Camponotus chrysurus	1			2	18		1		2	1		2
Camponotus melacnocnemis	4			2	8		1					
Camponotus spp.					5							
Paratrechina longicornis	69	8		21	18	1	3		1			
Paratrechina spp.					2		8	3		2		
Absence of ants			14		2	14	3		11	38		25
TOTAL	170	446	14	80	150	17	100	59	47	80	9	44
No. of maize plants		460			167			106			53	

The ant species distribution on the baits differed in the different growing conditions (Fig. 3). Except for the periphery versus center of the field (p=0.107), a two by two comparison resulted in significant differences in both of the other cases (Fig. 3). Along the walls, three pantropical species known as pests that nest in human dwellings (Hölldobler & Wilson 1990) competed for the baits (*Ph. megacephala*, 31.8%; *Tapinoma melanocephala* [F.], 19.4%; and *Pa. longicornis*, 40.6%), while in the urban gardens *M. opaciventris* was the most frequent (35% of the baits) and *T. melanocephala* was poorly represented (2.5%). At the periphery of the field we recorded a larger ant richness with *M. opaciventris* being the most frequent (16%), followed by *C. acvapimensis* (15%). Both of the latter species are ground-nesting savannah species which we frequently recorded in plantations (Leston 1973; Lévieux 1982; Suzzoni *et al.* 1994; Kenne & Dejean 1999).

The comparison of ant species distribution on the baits versus

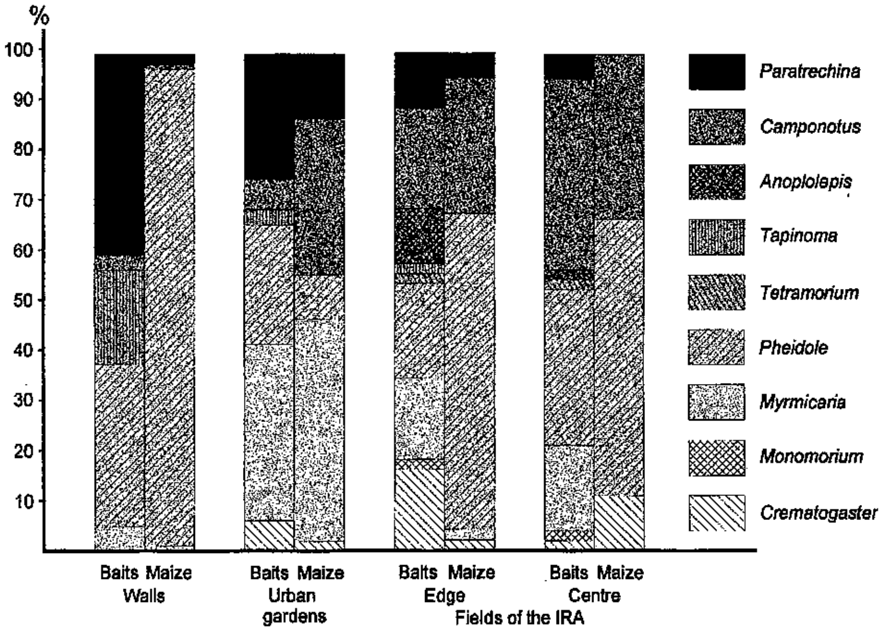

Fig. 3. Illustration of the competition between ant species for attending *P. maidis* thanks to a comparison between ant presence in the different studied areas (baits) and on maize plants (attending *P. maidis*). Statistical comparisons between the different milieu (Fisher exact test). Ant species on baits compared between growing conditions by the Montecarlo method: (1) general case: $p<10^{-5}$; (2) comparison 2 by 2; walls *vs.* urban gardens: $p<10^{-5}$; urban gardens *vs.* edge of the field: $p < 10^{-5}$; center *vs.* periphery of the fields: p=0.107. In each growing condition, comparison baits *vs.* maize: (1) walls: $p<10^{-5}$; (2) urban gardens $p<10^{-5}$; (3) periphery of the fields $p<10^{-5}$; (4) center of the fields p=0.39.

attending *P. maidis* on maize resulted in significant differences along the walls in the city, in the urban gardens and at the periphery of the field, but not in the center of the field (Fig. 3).

The competition between ant species to attend *P. maidis* on maize seems to be rather complex, as ploughing interferes in two growing conditions out of three. Along the walls in the city (ant nests undisturbed) *Ph. megacephala* had a tendency to occupy almost all the maize plants sheltering *P. maidis* (31.8% on the baits *vs.* 96.4% on maize plants; $p=1 \times 10^{-9}$) at the expense of *Pa. longicornis*, which was only recorded on 1.8% of the plants, and *T. melanocephala* which was absent. The urban gardens were unfavorable to both *Ph. megacephala* and *Pa. longicornis* (23.7% on the baits *vs.* 8.7% on maize plants; $p=0.002$; and 26.2% *vs.* 12%; $p=0.009$), but was favorable to competing *Camponotus* spp. (6.2% *vs.* 30.7%; $p=9 \times 10^{-6}$), while the presence of *M. opaciventris* was not significantly elevated (35% *vs.* 44%; $p=0.206$; tunnels not destroyed). At the edge of the field *Ph. megacephala* (13% *vs.* 61%; $p=9 \times 10^{-10}$) displaced both *M. opaciventris* (16% *vs.* 1.7%; $p=0.003$; tunnels destroyed) and *Crematogaster* spp. (15% *vs.* 3.4%; $p=0.018$), while the differences were not significant for *Paratrechina* spp. and *Camponotus* spp. (11% *vs.* 5.1%; $p=0.25$; and 19% *vs.* 27.1%; $p=0.32$). *Anoplolepis tenella* (Santshi) (11% on the baits), a ground-dwelling and foraging species (Dejean and Matile-Ferrero 1996), was absent on the maize. In the center of the field only nine maize plants were recorded with both *P. maidis* and ants, so comparisons resulted in non-significant differences. However, *Ph. megacephala* did appear to be exceptionally frequent on maize plants.

Correspondence analysis (Fig. 4) was used to compare ant distribution on baits and on maize plants attacked by *P. maidis*. We first built a 6 x 6 contingency table with six columns representing the types of situations (baits along the walls; in urban gardens; at the field edge; and maize plants attacked by *P. maidis* in the same three growing conditions) and six rows representing the ants (no ants; *M. opaciventris*; *Ph. megacephala*; *Camponotus* spp.; *Pa. longicornis*; other ant species). As the numbers of observations were very different from one growing condition to another, we used the proportions in the table, so that the six types of observations would have the same weight in the analysis. The results show a strong link between the type of growing condition and the ant species distribution ($f^2=0.81$). The first two axes contribute to 82% of the variance. The first axis (54% of f^2) opposes maize plants from urban gardens (21% of the variance of first axis) to maize plants situated along the walls (46%) and from the edge of the fields (18%). In terms of ants, this axis opposes *M. opaciventris* (25%), which is mostly

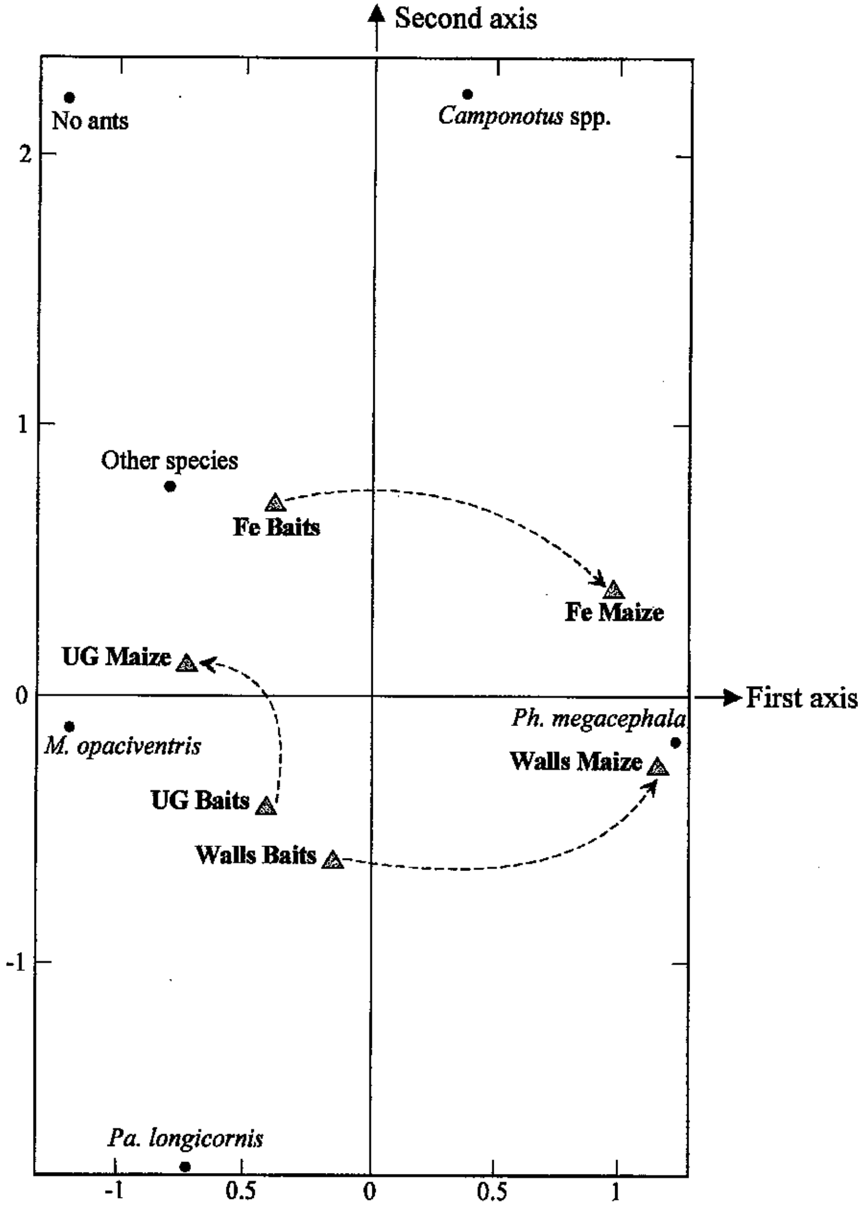

Fig. 4. Simultaneous representation of the distribution of the ant species and of six types of situations: baits along the walls; in urban gardens (UG); at the field edges (Fe); and maize plants attacked by *P. maidis* in the same three milieu) (correspondence analysis; SPAD 3.0 software).

present on maize plants from urban gardens, to *Ph. megacephala* (53%), mostly present on maize plants situated along the walls or at the field edges. The second axis (28% of f^2) opposes baits distributed along the walls (28%) and in urban gardens (13%) to those from field edges (35%). In terms of ants, this axis opposes *Pa. longicornis* (43%), which is mostly present on the baits distributed along the walls and in the urban gardens, to *Camponotus* spp. (38%), which is mostly present on baits from the field edges.

Hölldobler & Wilson (1990) noted that polygynous ant species fall into one of the following categories of specialization for nesting sites: specialized on (1) exceptionally short-lived nesting sites (opportunist species); (2) scarce nesting sites; (3) entire habitats that are long-lived, patchily distributed and extensive enough to support large populations. Among the four most frequent ant species of this study (all polygynous species with large colonies; present on 90.8% of the maize plants attacked by *P. maidis*), *Pa. longicornis* belongs to the first group; *Ph. megacephala* to both the first and the third group, while *C. acvapimensis* and *M. opaciventris* belong to the third group (see Lévieux 1982; Hölldobler & Wilson 1990; Suzzoni *et al.* 1994; Kenne & Dejean 1999). *Pa. longicornis*, characterized by swift-running workers very adept at rapidly locating new food sources, filling their crop and hurrying to recruit nestmates, but very timid in the presence of competitors (Hölldobler & Wilson 1990) was easily supplanted by others on maize plants (Fig. 3). In the same way, *T. melanocephala* which belongs to the same group, was supplanted by *Ph. megacephala* along the walls in the city, the only place where it was well represented.

Ph. megacephala, *T. melanocephala* and *Pa. longicornis* are known as «tramp species»: distributed widely by human commerce; they live in close association with man; are typically polygynous with «unicolonial populations» (i.e. absence of aggressiveness between individuals from different nests in an area, permitting the exchange of individuals between nests); and their workers are small and sterile (Passera 1994). Note that *M. opaciventris* shares several characteristics with tramp species (but is typically African and with relatively large polymorphic workers) (Suzzoni *et al.* 1994; Kenne & Dejean 1997, 1998a, b, 1999; Dejean *et al.* 1999; Kenne *et al.* 1999).

Ant species influence on the number of *P. maidis* individuals per maize plant

With the exception of *Crematogaster* sp. and *Ph. megacephala*, the number of *P. maidis* individuals per maize plant varied significantly as a function of the attending ant species (Fig. 5). Note that the difference between control plants (ants excluded) and those occupied by *Pa. longicornis* was not significant.

The survival of *P. maidis* when attended by ants can result from two factors. First, the ants consume honeydew and clean shelters, preventing the development of mould or even the homoptera drowning in their own waste material (Strickland 1947; Majer 1982; Rohrbach *et al.* 1988). Note that during their relationships with *P. maidis*, workers of *Pa. longicornis* mostly lick honeydew fallen onto the substrate and seem to be opportunistic, while workers of other species generally obtain honeydew directly from *P. maidis* individuals, build shelters over the homopterans and, in the case of *Ph. megacephala*, even transport brood to the shelters (Dejean *et al.* 1996). Second, ant protection of homopterans against predators such as coccinellids or parasitoids may occur, as has been noted by several authors (Barlett 1961; Way 1963; Bristow 1984; Beattie 1985). In the case of ant species able to occupy large territories, such as *Ph. megacephala*, protection generally results from the aggressiveness and/or the predatory activity of the workers against

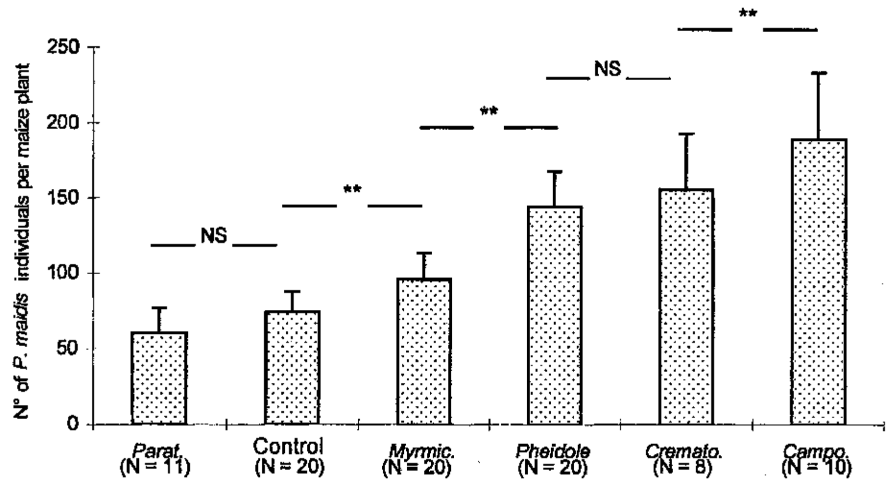

Fig. 5. Influence of five ant species on population sizes of *P. maidis* sheltered on 89 maize plants (mean±SE). Statistical comparisons: ANOVA:F(5; 83)=48.85; p<0.01.
Newman-Keuls test (F values):

	Control	*M. opacivent.*	*P. megaceph.*	*Crematog.* sp.	*C acvapimens.*
P. longicornis	2.2; NS	14.8; p<0.01	82.9; p<0.01	70.1; p<0.01	144.3; p<0.01
Control		7.8; p<0.01	81.6; p<0.01	63.4; p<0.01	146.5; p<0.01
M. opaciventris			39.9; p<0.01	34.2; p<0.01	96.5; p<0.01
P. megacephala				1.3; NS	22.3; p<0.01
Crematogaster sp.					8.2; p<0.01

all insects other than their nestmates and their trophobionts (see Jahn & Beardley 1994).

CONCLUSION

The present study identified that the rate of maize plants attacked by *P. maidis* was higher in the city of Yaoundé than in a field outside the city, with ants being a very important causal factor. We noticed that the more ant nests were affected by ploughing, the fewer maize plants were attacked by *P. maidis*. Thus, this study indicates that growing maize along the walls of the city must be avoided (as this preserves ant nests), that ant nests situated around urban gardens must be destroyed before planting maize, and that ploughing the earth over a large zone around the fields of maize limits the field edge effect.

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