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Life-history trade-off in two predator species sharing the same prey: a study on cassava-inhabiting mites

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In cassava fields, two species of predatory mites, *Typhlodromalus aripo* and *T. manihoti*, co-occur at the plant level and feed on *Mononychellus tanajoa*, a herbivorous mite. The two predator species are spatially segregated within the plant: *T. manihoti* dwells on the middle leaves, while *T. aripo* occurs in the apices of the plant during the day and moves to the first leaves below the apex at night.

To monitor the prey densities experienced by the two predator species in their micro-environment, we assessed prey and predator populations in apices and on the leaves of cassava plants in the field. Prey densities peaked from November to January and reached the lowest levels in July. They were higher on leaves than in the apices. To test whether the life histories of the two predator species are tuned to the prey density they experience, we measured age-specific fecundity and survival of the two predators under three prey density regimes (1 prey female/72 h, 1 prey female/24 h and above the predators level of satiation). *T. manihoti* had a higher growth rate than *T. aripo* at high prey densities, mainly due to its higher fecundity. *T. aripo* had a higher growth rate at low prey density regimes, due to its late fecundity and survival. Thus, each of the two species perform better under the prey density that characterizes their micro-habitat within the plant.

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Sympatric species that share a resource pose a challenge to ecological theory, because it is expected that the most competitive species will exclude the other. Species coexistence may arise from the joint occurrence of (1) temporal and spatial heterogeneity in the resource (Armstrong and McGehee 1980, Chesson and Huntly 1988, Namba 1993, Schmidt et al. 2000) or different availability of prey life stages (Haigh and Maynard Smith 1972) and (2) differential life-history or foraging adaptations of the competing consumers to resource availability (Abrams 1984, Chesson 1990, 1991, Wilson et al. 1999, Schmidt et al. 2000). The underlying assumption is the existence of a trade-off between different adaptations (Tilman 1989, Brown et al. 1994). Differential adaptations to resource density and distribution play an important role in the coexistence of competitors in many ecological systems (Wisheu 1998). In all cases, the underlying trade-off is inferred from comparisons among closely related species (Johnson and Hubbel 1975, Schmitt 1996) or from different lines (clones) within a species (Ebert and Jacobs 1991, Velicer and Lenski 1999).

In this paper, we measured life history traits of two closely related species of predatory mites co-occurring on individual cassava plants. The predatory mites *Typhlodromalus aripo* and *T. manihoti* feed upon the same

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herbivore, the cassava green mite (*Mononychellus tanajoa* or CGM), according to electrophoretic diet analysis (Bakker 1993). All three species are endemic to latin America, where they are widely distributed. In regions where other food sources are available, such as in Colombia, the two predator species show diet segregation (Bakker 1993). In some regions, only one of the predator species is present (e.g. *T. aripo* in southern Brazil; G. J. DeMoraes, pers. com.). However, in most regions both species co-occur and their diets overlap, as in northeast Brazil. This is also the case in western Africa, where both predator species have been introduced as biological control agents of CGM, a major cassava pest in that continent since the early 1970s. Since the last decade, *T. aripo* and *T. manihoti*, successfully control CGM populations and persist in African cassava fields (Yaninek et al. unpubl.). The coexistence of the two predator species is striking because they feed upon the same prey, and, moreover, belong to the same genus (Zacarias and Moraes 2001), which implies a high degree of similarity and probably intensifies competition.

In this article, we assess differential adaptations related to spatial segregation of the two predator species within the plant. *T. aripo* inhabits the apices and migrates to the leaves only at night (Onzo et al. 2003), whereas *T. manihoti* occurs exclusively on the leaves (Bakker and Klein 1992, Bonato et al. 1999). Based on our field observation that predators experience different prey densities within the plant, we hypothesize that, relative to *T. manihoti*, *T. aripo* performs better at low prey densities near the plant apex, whereas *T. manihoti* is relatively better at exploiting higher prey densities, typical of the middle leaves. We test this hypothesis by measuring species-specific population growth rates under high, intermediate and low prey density regimes in the laboratory. In the analysis, we explore how longevity and fecundity contribute to differences in growth rates between the species across prey regimes. Finally, we propose an underlying physiological mechanism that may explain the observed differences in life histories.

Material and methods

Field observations

Populations of CGM, *T. aripo* and *T. manihoti* on leaves and apices of cassava plants were monitored in a cassava field at Cruz das Almas, northeast Brazil, from August 1998 to August 1999. The field was selected such that the two main varieties planted in the region (Cigana Preta and Cidade Rica) were present and no intercropping occurred. Cigana Preta is a variety that reaches more than two meters height, has hard, elongated leaves and a medium-sized apex, while Cidade Rica usually does not exceed 1.5 meters in height, has soft, large leaves and a big and hairy apex. At each sampling event, the apices and leaves 2, 3, 7 and 8 (starting from the first leaf below the apex) from 5 plants of each variety were collected between 07:00 and 08:00 in the morning. All mobile stages of mites in the apex and of predatory mites on the leaves were collected, put in vials with 70% alcohol, and identified under the stereoscope at the Empresa Brasileira de Agropecuária (EMBRAPA). To assess CGM density on the leaves, we placed on each leaf a small cardboard square with a hole in the middle, the area of which was 1 cm^2, and counted the number of mobile stages inside that area. We repeated this procedure five times for each leaf. The placement of the square was random, except that care was taken that a maximum of lobes were sampled (cassava leaves are usually composed of 5 to 7 lobes). This method was calibrated by measuring the total number of CGM mobile stages on entire leaves and regressing the values obtained to the values found following our method ($N = 56$). We forced the regression through the origin. If significant, the regression coefficient could be used to obtain an estimate of CGM densities on the leaves. Field samples were taken twice per month, but we lumped the data to obtain one estimate per month.

Cultures

Cassava (CMC40 variety) was shipped from Colombia (CIAT) and grown in a greenhouse at 25°C, 70% RH and 16L/8D photoperiod. Plants were planted as stakes (ca 20 cm) in $20 \times 20 \times 20$ cm plastic pots, with soil and a 28N, 14K, 14P fertilizer. They were grown for a maximum of three months to keep plant size within limits. CGM was reared on entire plants, in a separate greenhouse compartment. Clean plants were infested by putting CGM-infested leaves at the base of one or more leaf petioles. The predatory mites *T. aripo* and *T. manihoti* were shipped by the International Institute of Tropical Agriculture (IITA) from Benin, and reared in a climate room under the same conditions as in the greenhouse compartments. They were kept in $25 \times 25 \times 10$ cm aerated plastic boxes, on a hard plastic arena surrounded by wet cotton to increase humidity (Mégevand et al. 1993) and fed three times a week with two CGM-infested leaves. Every three months, cultures were supplemented with specimens collected in the field and sent by IITA.

Life-history experiments

All experiments were performed in the climate room used for the predator cultures. To measure predation

rates on adult female prey, we produced cohorts of the two predator species by letting females oviposit on CGM-infested cassava leaves during 24 h. Then, females were removed and eggs developed until adulthood. At day 13, we picked 13 females of each species and placed them individually on leaf discs with 25 adult female prey. Oviposition and predation were measured on day 13, 14 and 15 (corresponding to the peak of oviposition). Every day, predator females were transferred to a new leaf disc with the same prey regime. We calculated conversion rates by taking the ratio of oviposition to predation per day for each individual (thus ignoring partial ingestion). We did not measure the rates of predation of both predators on eggs and juveniles because it is known that they consume equal amounts of these prey stages (R. Hanna, pers. comm.).

Next, we measured life histories of the two predator species under different regimes of prey density on cassava leaf discs (∅ 2 cm). Egg cohorts of *T. aripo* and *T. manihoti* were produced by well-fed females placed on CGM-infested cassava leaflets for 24 h. Then, predator eggs were collected individually, placed on a clean leaf disc floating on wet cotton and assigned to three different prey regimes: 1 adult female prey per 72 h (low prey density regime), 1 adult female prey per day (intermediate prey density regime) and more than 20 female prey and all other prey stages in high but unspecified numbers (high prey density regime). Every day, predators were transferred onto a new cassava leaf disc with the same prey regime.

To assess the developmental time under intermediate and low prey density regimes, an immature prey stage was offered instead of the more difficult-to-capture adult female. Near maturation (four days after egg hatching), predators were offered adult female prey (and thus also the eggs they laid before being killed by the predator). This ensured that prey was always eaten. As soon as predators developed into the deutonymph stage, we placed one male on each leaf disc. Every day, males were re-assorted to discs with other females to prevent non-mating due to individual incompatibilities. Males were removed after females laid their first egg. Adult female predators were offered the same prey regime as during their development, and oviposition was assessed daily. Sex ratio was assessed as the proportion females among the offspring that successfully matured (secondary sex ratio).

During the test period, some mites escaped from the experimental set-up. If escape occurred during the developmental period, those individuals were discarded. If they escaped during the oviposition period, they were taken into account for calculating daily oviposition until escape, but not for assessing longevity. Sample sizes (not including escapes) ranged from 12 to 54 individuals (see legend of Fig. 2).

Growth rate and LTRE analysis

The finite rate of increase (λ) of each species under different prey densities was calculated using the Euler-Lotka equation (Carey 1993). At low prey densities, increased mobility leads to random mating. Under these conditions, sex allocation theory predicts a 1:1 sex ratio. Experiments on different mite species confirm this prediction (Sabelis 1985, Sabelis and Nagelkerke 1988, Nagelkerke and Sabelis 1998, Toyoshima and Amano 1998). Therefore, we assumed a 1:1 sex ratio at low prey densities. All other variables were measured explicitly (see life-history measurements).

Because the growth rate lumps many life history variables, each associated with a particular error, we estimated confidence intervals by bootstrapping (Meyer et al. 1986).

Differences in reproduction and survival at different ages do not translate directly into differences in the growth rate (e.g. Caswell 1989). We performed a life table response experiment analysis (LTRE analysis) to understand which lower-level changes in the life histories of *T. aripo* and *T. manihoti* contributed to the differences in growth rates across prey regimes (Caswell 1989, 2001). LTRE analysis is analoguous to an ANOVA, but quantifies the deviations (due to treatment) from the overall average using sensitivity analysis instead of sum-of-squares (Caswell 2001). We considered species and prey regime as two fixed effects, s and e (species and environment), and used the overall-mean matrix $L^{(\cdot\cdot)}$ as the reference matrix. Denoting $L^{(se)}$ as the Leslie-matrix of the life history resulting from treatment combination (se), the model is

$$\lambda^{(se)} = \lambda^{(\cdot\cdot)} + \alpha^{(s)} + \beta^{(e)} + (\alpha\beta)^{(se)}$$

where $\lambda^{(se)}$ is the λ estimated by the model and the $\lambda^{(\cdot\cdot)}$ dominant eigenvalue of the reference matrix $L^{(\cdot\cdot)}$, $\alpha^{(s)}$ and $\beta^{(e)}$ denote the main effects and $\alpha\beta^{(se)}$ the interaction. These effects are then decomposed in the age-specific reproductive and survival contributions, which approximate an observed change in λ, due to the contributions of each matrix element a_{ij}. The main effects and interactions are calculated as the sum of all contributions, according to

$$\alpha^{(s)} = \sum_{i,j} (a_{ij}^{(s\cdot)} - a_{ij}^{(\cdot\cdot)}) \left.\frac{\partial \lambda}{\partial a_{ij}}\right|_{\frac{1}{2}(L(s\cdot) + L(\cdot\cdot))}$$

$$\beta^{(e)} = \sum_{i,j} (a_{ij}^{(\cdot e)} - a_{ij}^{(\cdot\cdot)}) \left.\frac{\partial \lambda}{\partial a_{ij}}\right|_{\frac{1}{2}(L(\cdot e) + L(\cdot\cdot))}$$

$$\alpha\beta^{(se)} = \sum_{i,j} (a_{ij}^{(se)} - a_{ij}^{(\cdot\cdot)}) \left.\frac{\partial \lambda}{\partial a_{ij}}\right|_{\frac{1}{2}(L(se) + L(\cdot\cdot))} - (\alpha^{(s)} + \beta^{(e)})$$

where $\partial\lambda/\partial a_{ij}$ is the sensitivity, calculated – for main effects – at a matrix mid-point between the average

treatment (s or e) matrix and the reference matrix, or – for the interaction – mid-point between observed and reference matrix. An interaction represents a contribution in addition to an additive model ($\alpha + \beta$).

Results

Field observations

The pattern of annual fluctuation of predators and prey populations on cassava does not show major differences between the two varieties studied (Fig. 1). CGM populations exhibited a peak between November and December, both in apices and leaves and in the two varieties. Populations of *T. aripo* reached a maximum in March, those of *T. manihoti* did not present a particular annual pattern. The two predator species were found in different plant strata: *T. aripo* occurred exclusively in the apices, *T. manihoti* on the leaves.

The regression for the calibration of the method used to count CGM on the leaves yielded a good fit ($F_{1,55} = 41.7$; $p < 0.0001$). Prey populations were consistently higher on the leaves than in the apices. Indeed, the peak density was 516 and 347 mobile stages on the leaves of Cigana Preta and Cidade Rica, respectively, while the maximum reached on the apices were of 17 and 14, respectively. Moreover, during most of the year, no CGM was found in the apices, while on the leaves between 10 and 100 CGM individuals occurred. At the plant level, these differences in density translate into bigger differences in abundances, since one plant has only one to three apices, yet more than ten leaves.

Predation and life-history experiments

When offered 25 adult CGM per day, *T. manihoti* killed more CGM than *T. aripo* did (Table 1; Anova, $F_{1,24} = 4.28$, $p < 0.001$). *T. aripo* converted more efficiently the prey eaten into eggs. Because we had no means to estimate partial ingestion, this result indicates either higher conversion rate or higher feeding efficiency (i.e. less partial ingestion). In any case, it shows that *T. aripo* needs less prey to produce the same number of eggs as *T. manihoti*.

Across all prey regimes, *T. manihoti* had shorter developmental time than *T. aripo* (Fig. 2a, c, e): on

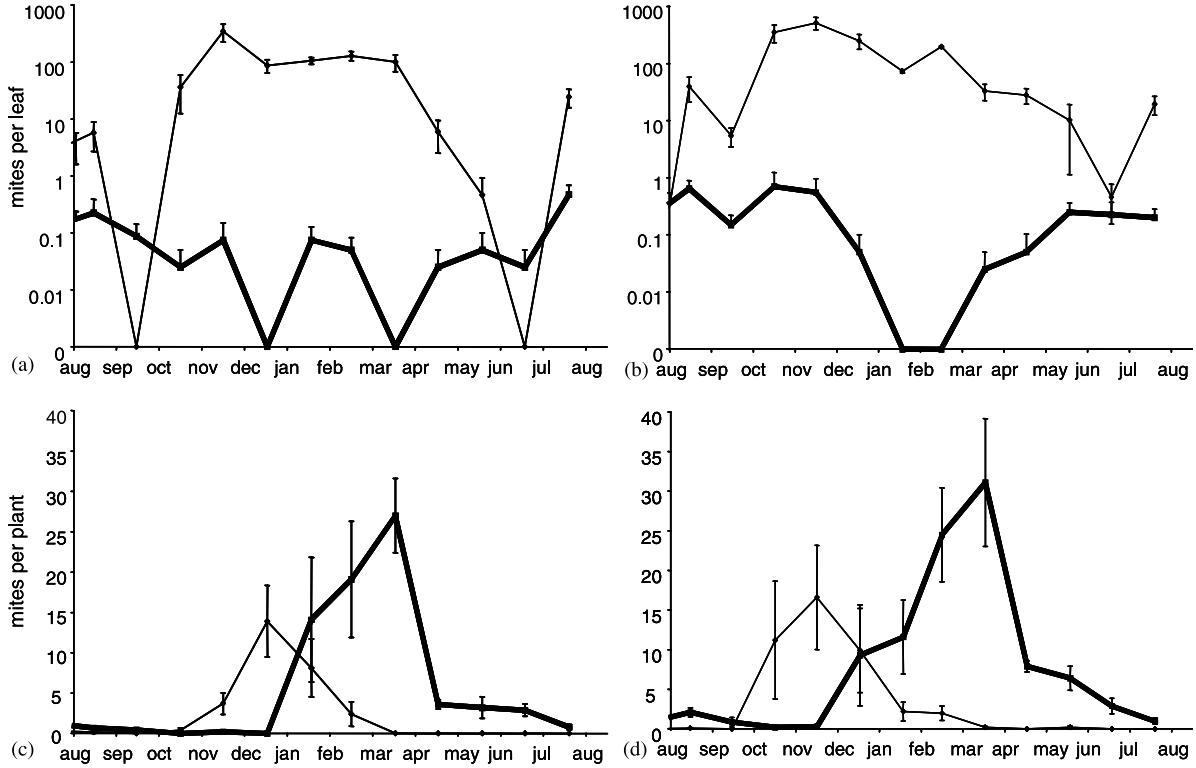

Fig. 1. Population dynamics of CGM, *T. aripo* and *T. manihoti* from August 1998 to August 1999. Thin lines represent the dynamics of the mobile stages of CGM, thick lines correspond to the mobile stages of predators (*T. manihoti* in Fig. 1a and b, *T. aripo* on Fig. 1c and d, respectively). Fig. 1a and b: mite populations on leaves; Fig. 1c and d: mite populations on the apices. Fig. 1a and c: mites on the variety Cidade Rica; Fig. 1b and d: mites on the variety Cigana Preta. Vertical bars indicate standard errors of the mean. Note differences in scale.

Table 1. Sex ratio and foraging-related traits of predators in an arena with 25 adult female prey/day. Values represent averages over ages 13, 14 and 15, corresponding to the peak of oviposition. Sex ratios are calculated over the whole life span.

Trait	*T. manihoti* (mean ± sd)	*T. aripo* (mean ± sd)
Predation rate (prey/day)	15.97 ± 2.81	1.69 ± 0.95
Oviposition rate (eggs/day)	3.77 ± 0.78	0.61 ± 0.65
Conversion rate (eggs/prey)	0.23 ± 0.06	0.39 ± 0.42
Sex ratio	0.82 ± 0.059	0.66 ± 0.09

average, it started its oviposition period 3 to 5 days before *T. aripo*. Its oviposition rate was also higher (Fig. 2a, c). However, *T. aripo* continued egg production for a longer period. By the time *T. manihoti*'s cohort had ceased laying eggs, the *T. aripo* cohort was still to lay 30% of its eggs at high prey density, and nearly 50% at intermediate prey density. In the low prey density regime, all *T. aripo* eggs were laid later than the only egg laid by the females in the cohort of *T. manihoti*. Total fecundity of *T. manihoti* at high prey density was approximately three times higher than that of *T. aripo* (on average 16.5 versus 6.5 eggs per female, respectively). At intermediate prey density, this difference was reduced: compared to the high prey density regime, the average fecundity of *T. manihoti* dropped to 9 eggs per female, whereas that of *T. aripo* increased slightly to 6.9. The fecundity of the two species was drastically reduced when prey density was low: the whole *T. aripo* cohort laid more eggs than the *T. manihoti* cohort (3 eggs out of 33 females versus 1 egg out of 54 females, respectively).

The areas between the longevity curves (Fig. 2b, d, f) correspond to the difference between the longevities of the two predators. *T. aripo* survived longer than *T. manihoti*, regardless of prey regime. For example, in the intermediate prey density regime, the average age at which 50% of the cohort was still alive was approximately twice the value for *T. aripo* than for *T. manihoti*.

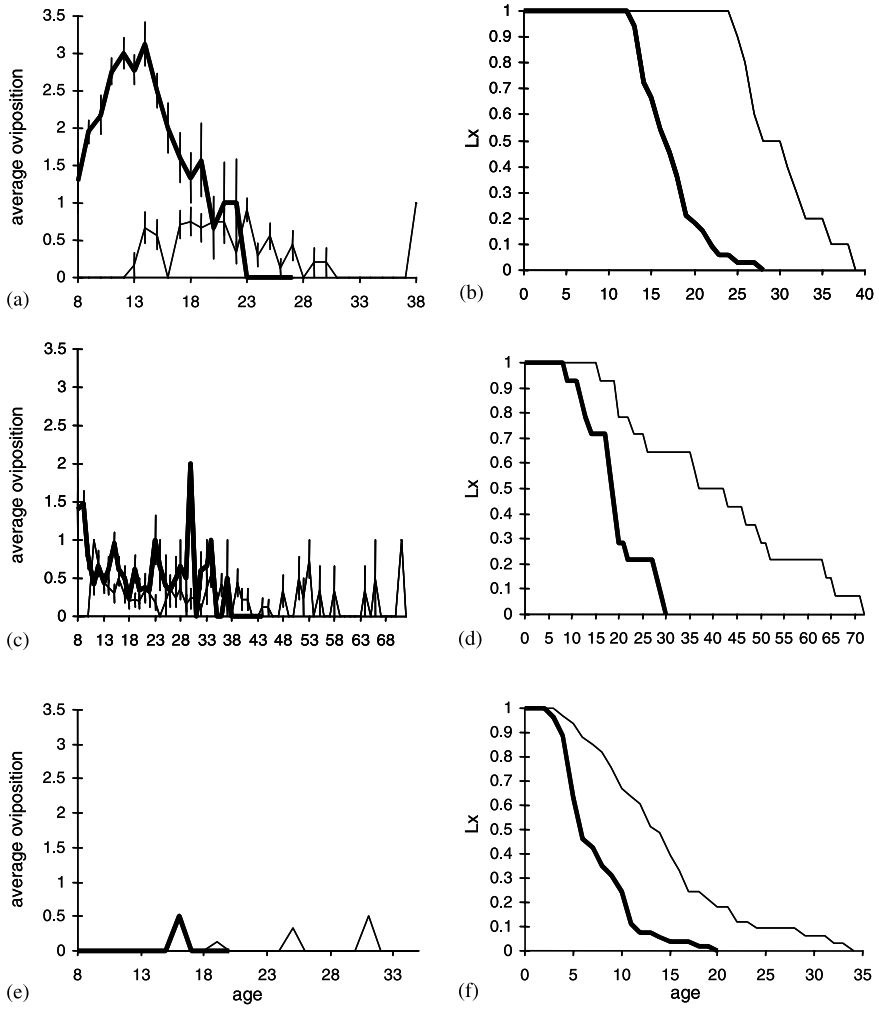

Fig. 2. Life history traits of *T. aripo* (thin lines) and *T. manihoti* (thick lines) under different regimes of prey density. Fig. 2a, c and e: daily oviposition; Fig. 2b, d and f: longevity (proportion of individuals alive at day x). Fig. 2a and b: high prey density; Fig. 2c and d: intermediate prey density; Fig. 2e and f: low prey density. For the same prey regime, individuals used for the cumulative oviposition curve are the same as the individuals used for the longevity curve, except the ones that escaped, which are only included in the fecundity. Vertical bars indicate standard errors of the mean. Sample sizes for *T. aripo*: 1a – 12, 1b – 12, 1c – 22, 1d – 14, 1e – 33, 1f – 33; sample sizes for *T. manihoti*: 1a – 38, 1b – 21, 1c – 41, 1d – 12, 1e – 54, 1f – 54.

Growth rate and LTRE analysis

The growth rate of *T. manihoti* was considerably higher than that of *T. aripo* when prey density was high (Fig. 3). At intermediate prey density, this difference in growth rates decreased. In fact, while the growth rate of *T. aripo* did not vary as prey density shifted from the high to the intermediate regime, that of *T. manihoti* decreased from 1.25 to 1.16. When prey density was low, the difference between the growth rates of the two species was reversed, with *T. aripo* having a higher growth rate than *T. manihoti*. Across the three prey regimes, the growth rate of *T. manihoti* varied from 0.83 to 1.25, while the variation in the growth rate of *T. aripo* was smaller (from 0.92 to 1.08).

The LTRE analysis yielded a satisfactory fit to the data, since the estimates of the growth rate fall within the confidence intervals of the growth rate calculated from the life-history data (Fig. 3). Differences in reproduction and survival after day 30 contributed little to differences in population growth (Fig. 4–7).

Over all prey regimes, the main differences in growth rate between *T. aripo* and *T. manihoti* were due to the fertility contribution around the age of 10 days (Fig. 4), where *T. manihoti* clearly outperformed *T. aripo* (Fig. 2). To some extent, *T. aripo*'s lower fecundity was

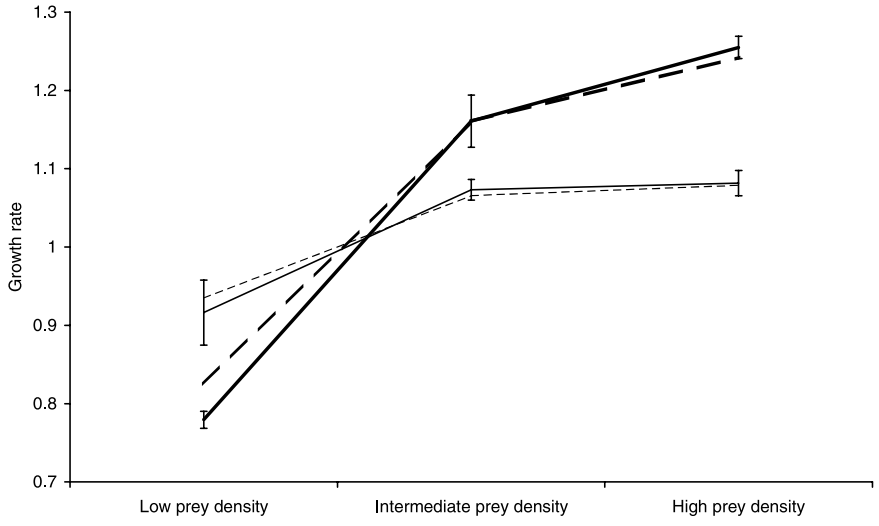

Fig. 3. Species-specific growth rate (λ) of *T. aripo* (thin lines) and *T. manihoti* (thick lines) under different regimes of prey density. Solid lines correspond to growth rates calculated from the measured life histories, dashed lines to growth rates predicted by the Leslie matrix and used in the LTRE analysis.

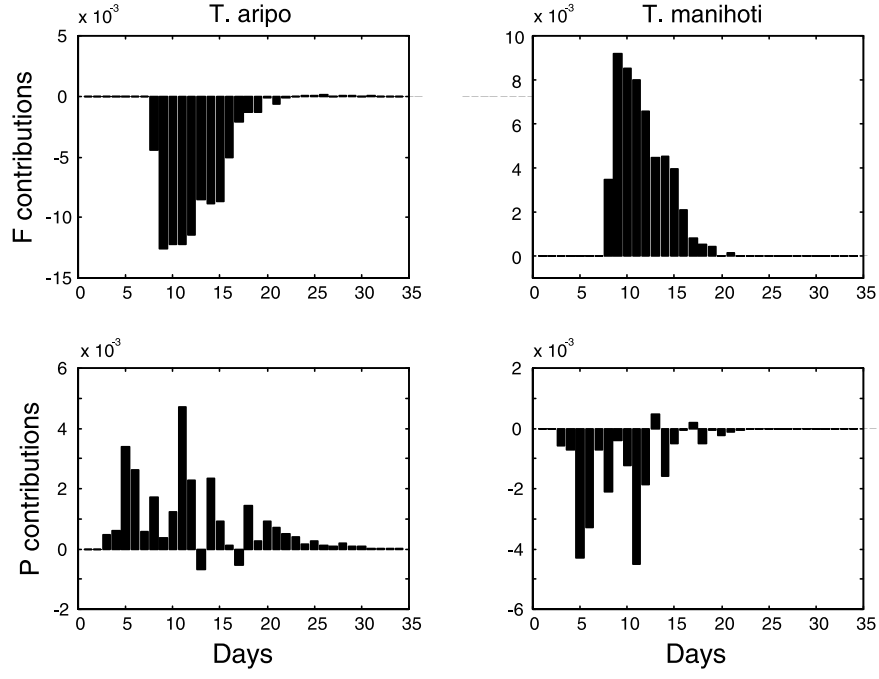

Fig. 4. Age-specific contributions to the population growth rate (λ), made by the differences in fertility (F contributions, panels in top row) and survival (P contribution, panels in bottom row) between the mite species (*T. aripo* and *T. manihoti*) relative to the overal mean. Note differences in scale.

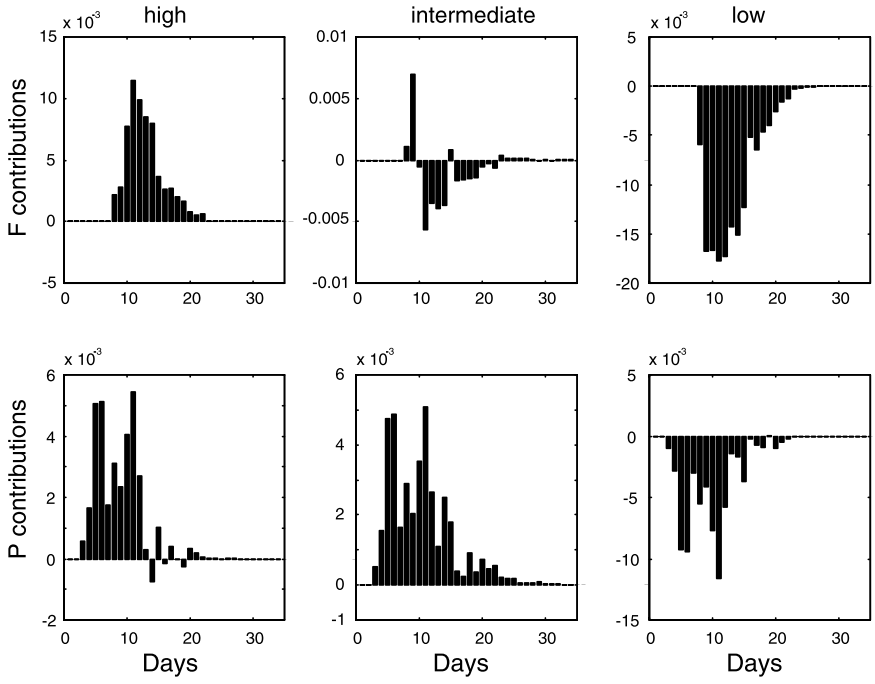

Fig. 5. Age-specific contributions to the population growth rate, made by the differences in fertility (F contributions, panels in top row) and survival (P contributions, panels in bottom row) across the three environments (high, intermediate and low prey density) relative to the overal mean. Note differences in scale.

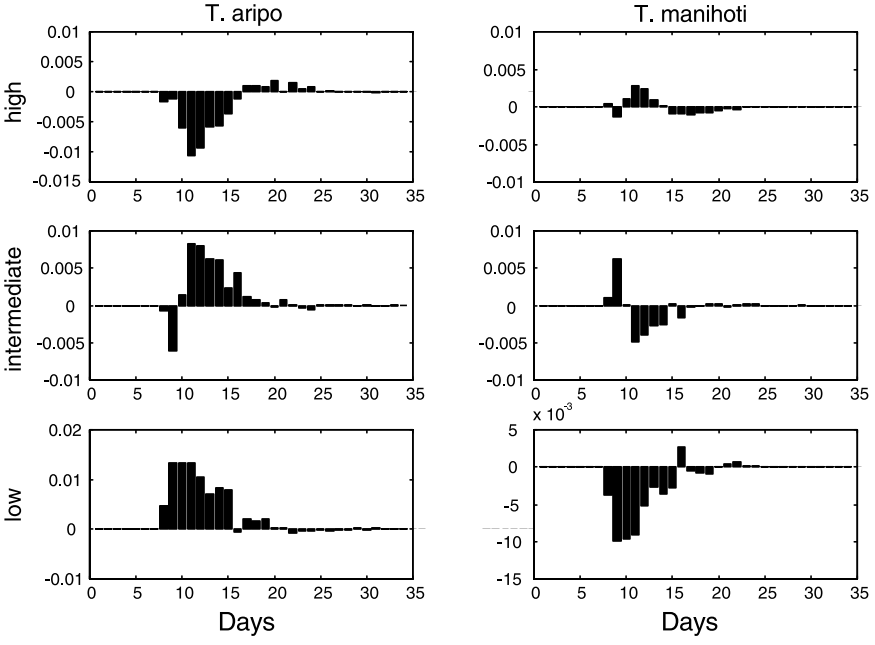

Fig. 6. Age-specific contributions to the population growth rate, due to the interaction of species (*T. aripo* and *T. manihoti*) and environment (high, intermediate and low prey density) in the fertility components. Note differences in scale.

compensated by its higher survival between day 5 and 25 (Fig. 4). For the main effect of prey density, the decrease in the growth rate of the two species from the high to the intermediate prey density regime was mainly due to changes in fecundity after day 10 (Fig. 5, top row). However, the low growth rate at low prey density was due to both fecundity and survival components. The species–environment interaction was largely due to fertility components (Fig. 6 and 7, note the differences in scale). Positive contributions to the growth rate of *T. aripo* were small and came from late fecundity and survival. As prey density declined, *T. aripo*'s fertility, especially between day 10 and 15, kept its growth rate relatively stable across environments. In the low prey density regime, its survival between days 5 and 12 also made important contributions to the growth rate. The high growth rate of *T. manihoti* under high prey density was due to its survival in the early age classes (7 to 14),

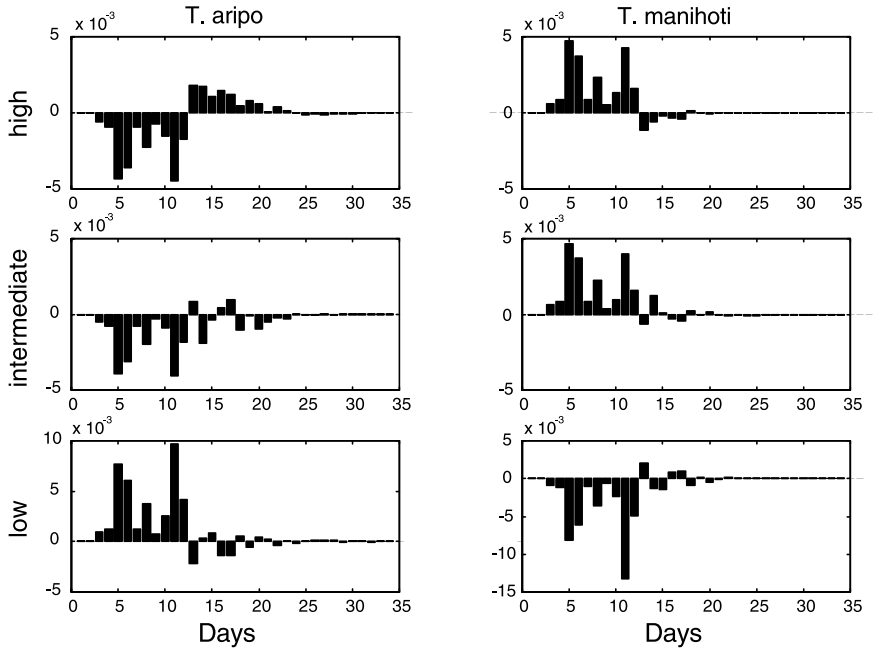

Fig. 7. Age-specific contributions to the population growth rate, due to the interaction of species (*T. aripo* and *T. manihoti*) and environment (high, intermediate and low prey density) in the survival components. Note differences in scale.

and to its fecundity between days 11 and 14. Survival contributions in the intermediate prey density regime followed the same pattern, while the fecundity contributions shifted to days 8 and 9 (Fig. 2). In the low prey density regime, there were virtually no positive contributions to the growth rate of *T. manihoti*.

Discussion

Our field observations reveal that cassava plants harbour higher densities of CGM on leaves than in the apices, irrespective of the season. Predators of CGM are found on different parts of the plant: *T. aripo* in the apices and *T. manihoti* on the leaves. Our laboratory experiments show that *T. aripo* outperforms *T. manihoti* at low prey density, and the reverse occurs when prey density is high (Fig. 3). Thus, each predator species has life-history traits that allow them to successfully exploit the prey densities typically found in their respective microhabitat.

Although the growth rates of the two predator species qualitatively fit their distribution pattern within cassava plants, additional factors need to be invoked to understand the population densities found in our field observations. In fact, despite its high growth rate when density is high, and the high prey densities on the leaves, *T. manihoti* is not abundant (around 1 per leaf). This may be due to its strict humidity requirements: *T. manihoti* is mostly found in swampy areas in Africa (Onzo et al. 2003), thus our study area may have been too dry to harbour high densities of *T. manihoti*. In addition, populations of *T. aripo* reach numbers that cannot be solely explained by their predation upon CGM present in the apex, since the population peak of *T. aripo* exceeds the maximum number of CGM in the apex. To complement its diet, *T. aripo* may migrate to the lower strata at night and feed upon CGM on the leaves. Indeed, *T. aripo* is found on the leaves at night in African fields (Onzo et al. 2003), and the function of this diurnal migration may be to forage. Moreover, CGM may migrate into the apex and be predated upon by *T. aripo*. Indeed, greenhouse experiments showed that CGM migrates to the upper strata, both in presence and absence of *T. manihoti* on the leaves (Magalhães et al. 2002). In addition, *T. aripo* may complement its diet with plant-borne material. It is known that it feeds upon plant exudate (Bakker 1993) and plant cell contents (Magalhães and Bakker 2002). Adding cassava exudate to their diet increases their egg production (Bakker 1993), but to what extent this plays a role in natural populations is still unknown.

Differences in the predators' growth rates at different prey densities stem from differences in foraging and life-history traits between predator species. *T. manihoti* is more close to an r-strategy than *T. aripo* is: it has a high rate of prey intake and rapidly converts prey into offspring, by starting reproduction early in life and by producing eggs at a fast rate. This leads to a higher fecundity and growth rate of *T. manihoti* at high prey densities relative to *T. aripo*. The growth rate of *T. manihoti* drops off sharply when prey densities decline. At low prey densities, *T. aripo* outperforms *T. manihoti*, due to its fecundity and survival. Across all prey regimes, *T. aripo* has higher survival than *T. manihoti*.

Under natural conditions – where prey shows fluctuations in abundance – a longer life span is to the advantage of *T. aripo* when prey is scarce, since it increases the probability of remaining alive on a cassava plant until more prey arrives. Moreover, *T. aripo* decreases its oviposition rate from the high to the intermediate prey density regime, which is not associated with a reduction in fecundity but rather with an extension of the oviposition period (and concomitantly of the life span, since the post-oviposition period is virtually absent). This suggests that *T. aripo* reduces its metabolic rate as prey density decreases, leading to parsimonious allocation of resources to egg production and activity. The extension of the oviposition period and life span under low prey densities has been observed in other studies with insects (Slansky 1980) and predatory mites (Blommers and Arendonk 1979, Sabelis 1981, Sabelis and Meer 1986). However, the growth rate of *T. aripo* is low when prey density is high. This is very uncommon in predatory mites that are typically r-selected (Sabelis and Janssen, 1994) and whose predation and growth rates under high prey density are much higher than those of *T. aripo* (Janssen and Sabelis 1992).

Life history adaptations may explain how each predator species thrives in their respective microhabitat, but what precludes them to invade the other microhabitat? That is: why are the life histories of these predators not plastic enough to maximize growth rate at both high and low prey densities? Indeed, there are examples of life histories that vary between high and low productivity habitats (Jordan and Snell 2002). In our study, each predator species shows a certain degree of plasticity in life history traits across environments. However, within each environment, it is never such that *T. manihoti* has higher survival than *T. aripo* nor that *T. aripo* has higher developmental or oviposition rate than *T. manihoti*. Since these life-history traits determine the predators' performance at low and high prey densities, we would expect plasticity to evolve, unless a physiological or genetic trade-off imposes too high a cost (Lessels 1991, Zera and Harshman 2001). Our results suggest that the trade-off lies in the metabolic rate: *T. aripo* has a low metabolic rate, which allows this species to survive for long periods of time, but impedes it to have a high oviposition and developmental rate. In contrast, *T. manihoti*, with a high metabolic rate, rapidly consumes prey and converts it into eggs, but this goes at the cost of survival. This hypothesis is confirmed in life-history selection experiments with other species of phytoseiid mites (Sabelis, unpubl.).

Alternative to the trade-off hypothesis is the possibility that other characteristics of the two microhabitats in cassava have constrained the distribution of these predator species within the plant. Subsequently, each predator would have developed life-history adaptations to prey densities pertaining to the microhabitat where they dwell.

Whether the two predatory mite species coexist on cassava plants due to each predator species outperforming the other at certain prey densities (Brown 1989, Schmidt et al. 2000) remains an open question.

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