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# Saturation deficit tolerance spectra of phytophagous mites and their phytoseiid predators on cassava

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## ABSTRACT

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In South America, phytophagous cassava mite populations reach high densities during the dry season but occur in low numbers during the rainy season. Some of their phytoseiid predators, however, show the reverse pattern. We test the hypothesis that this different seasonal phenology can be attributed to distinct saturation deficit tolerance spectra. Eggs of various species c.q.. strains of phytoseiids, originating from different climate zones, were screened for their tolerance to a range of saturation deficits and compared with the tolerance spectrum of tetranychid species collected from cassava. In total 19 species/strains of predatory mites were compared with six tetranychid species. The response curves for all predators were sigmoidal with a narrow and specific region of saturation deficits where egg hatch success fell from 100% to 0%. Using probit analysis this region was characterized by the $SD_{50}$, the saturation deficit at which only 50% of the eggs hatch. The response curves for the herbivores were trapezoid. In contrast to the phytoseiids the latter do not differ in the range of saturation deficits tolerated, but in the magnitude of the response.

It appeared that inter-strain differences in the Phytoseiidae are sometimes larger than interspecific differences. We demonstrate that there is a significant correlation between population-specific $SD_{50}$-values and long term average relative humidity in the collection site. The implications of this finding are discussed in terms of condition specific competition.

## INTRODUCTION

Pest outbreaks often coincide with dry, warm weather (*cf.* Mattson and Haack, 1987). This observation certainly applies to spider mites (Tetranychidae). Outbreaks of these pests are favoured by hot, dry weather, whereas highly humid conditions tend to preclude major damage to plants (Boudreaux, 1958). The tetranychid *Mononychellus tanajoa* (Bondar), commonly called the cassava green mite (CGM), was accidentallly introduced into Africa and spread rapidly over the African cassava belt (Yaninek and Herren, 1988) causing recurrent serious yield losses (Yaninek *et al.*, 1990; Herren and Neuenschwander, 1991). In general, CGM populations increase rapidly at the beginning of the dry and wet season (Yaninek *et al.* 1989b), followed by a dramatic decline as the wet season progresses. Seasonally dry areas (4-6 dry months per year) run the greatest risk of severe CGM infestations (Yaninek and Bellotti, 1987). Host plant quality, temperature, rainfall and the lack of effective natural enemies are mentioned as major factors influencing pest dynamics in Africa (Yaninek *et al.* 1987, 1989ab).

In South America, cassava's continent of origin, more than 50 species of phytophagous mites have been found on this crop (Byrne *et al.* 1983). The most frequently reported are the tetranychids *M. tanajoa*, *M. caribbeanae* (McGregor), *Tetranychus urticae* Koch, *T. cinnabarinus* (Boisduval), *Oligonychus peruvianus* (McGregor) and *O. gossypii* (Zacher). Moderate-to-high populations of these mites are most commonly found in ecological zones with a pronounced dry season, particularly in seasonally dry regions with more than 4-6 dry months per year (Bellotti *et al.*, 1987). *Mononychellus tanajoa* can cause yield losses of 10-50% in subhumid areas of Northeast Brazil (Veiga, 1985, Guerrero *et al.*, 1992), and *M. carribeanae* is a major biotic constraint on production of cassava in semiarid areas of Ecuador (Braun *et al.*, 1992) and Colombia (Byrne, 1980). In Northeast Brazil phytoseiid species diversity is low compared to that in other parts of CGM's range. However, even high phytoseiid species diversity, as occurs in semiarid areas of Ecuador, does not always result in an acceptable level of natural biological control of *M. carribeanae* (Braun et al., 1992). In subhumid cassava-growing areas of the Americas, conservation and enhancement of phytoseiids is an important strategy in management of *Mononychellus* species (Braun et al., in press)

To achieve a permanent and adequate suppression of the cassava green mite in Africa, the International Institute of Tropical Agriculture (IITA) in Nigeria/Benin adopted the strategy of classical biological control (Yaninek and Herren, 1988; Yaninek *et al.* 1992). In search for natural enemies of CGM emphasis has been on predaceous mites of the family Phytoseiidae. Extensive explorations in most cassava-growing areas of the Neotropics have found more than 50 species of Phytoseiidae in association with CGM (Moraes *et al.*, 1982, 1988, 1991; Byrne *et al.*, 1983; Moraes and McMurtry, 1983; Bellotti *et al.*, 1987; Moraes and Mesa, 1988).

The most widely distributed of these predators is *Typhlodromalus limonicus s.l.* (Garman and McGregor). However, field censuses showed that populations of this predatory mite are higher during the rainy season than during the dry season when they may disappear (Noronha and Moraes, 1989, but see Herrera, 1992). This decrease in predator numbers typically parallels an increase in prey numbers that may lead to economically significant pest outbreaks in South America (Bellotti *et al.*, 1985). The decline of this phytoseiid mite during these periods of prey abundance suggests an inhibiting effect of climatic conditions.

In most regions where cassava is cultivated, the climate is characterized by relatively constant temperatures. The temperature changes during the year are often smaller than the daily fluctuations. Although altitude and other topographical factors exercise a strong influence on mean annual temperature, the season is defined by humidity and rainfall rather than by temperature. Hence, if the key factor determining the observed overall predator dynamics is abiotic, it probably is humidity or rainfall. This is not unlikely, as it follows from the literature that, relative to their tetranychid prey, phytoseiids are much more susceptible to dry conditions (*e.g.* Stenseth, 1979; Sabelis, 1981; Ferragut *et al.*, 1987; Kramer and Hain, 1989). In this paper we test the hypothesis that the difference in seasonal phenology between phytophagous cassava mites and their phytoseiid predators can be attributed to a distinct saturation deficit tolerance spectrum. The eggs of various species *c.q.* strains, originating from different climate zones, were screened for their tolerance to a range of saturation deficits and compared with the tolerance spectrum of their tetranychid prey. In total 19 species/strains of phytoseiids were compared with 6 tetranychid species.

Comparative analyses of the phytoseiid mite complex on cassava in different ecological zones in Brazil and northern South America showed that species tend to separate out along ecological gradients such as the number of dry months per year (CIAT, 1992). This observation is supported by data in the literature showing that phytoseiids from dry areas are more resistent to low humidities than are phytoseiids from humid areas. Interspecific differences (*e.g.* McMurtry and Scriven, 1965; McMurtry, 1980; Bounfour and McMurtry, 1987; Dinh *et al.*, 1988), as well as differences between geographical subpopulations of the same species (McMurtry et al., 1976; McMurtry, 1980; Perring and Lackey, 1989) are found. Therefore, the second hypothesis tested was that along the gradient from humid to dry habitats phytoseiid species/strains can be characterized by an increasing tolerance to high saturation deficits. This was done by multiple regression of $SD_{50}$ on long term average metereological data, such as average annual rainfall, relative humidity, vapour pressure deficit and number of dry months per year.

## MATERIALS AND METHODS

The effect of different saturation deficits on the cassava-inhabiting mites was tested on eggs only. The response tested was quantal, *viz.* the fraction of eggs that had or had not hatched after exposure to a predefined and constant humidity regime for a period of time. The experimental period always exceeded the developmental time. In practice this meant that the number of hatched and shrivelled eggs was recorded after three days for phytoseiids and after six days for tetranychids. All experiments started with a cohort of eggs less than 24 hours of age. All species or strains were obtained from lab colonies, with the exception of *Typhlodromalus aripo* De Leon and one strain of *T. limonicus s.l.*, that were collected in the field,

The eggs of 19 strains of phytoseiids belonging to 10 species were tested (see

Table 1). It should be stressed that the *T. limonicus* from USA and Jaguariuna are reproductively incompatible with the other strains. Because they represent a distinct species (Braun et al. in press); they will be given the affix *s.s.* to distinguish them from the other species (*T. limonicus s.l.*). Electrophoresis reported other biological data indicating that the different strains of *T. limonicus s.l.* were distinct subpopulations (Cuellar, 1992; Cuellar, *et al.*, in press). The phytoseiids were

TABLE 1

Phytoseiid species and strains used in the experiments.

| Species | Origin | Date of colection | Prey used in culture |
|---|---|---|---|
| *Cydnodromella pilosa* (Chant) | Pico de Oro,MEX | May 1987 | *Tetranychus urticae* |
| *Neoseiulus californicus* (McGregor) | Bogotá, COL | July 1986 | *T. urticae* |
| *Neoseiulus idaeus* Denmark & Muma | Fonseca, COL<br>Petrolina, BRA | 1988 &1990<br>1988 | *Mononychellus caribbeanae* and *T. urticae* |
| *Phytoseiulus macropilis* (Banks) | Recife, BRA | 1988 | *T. urticae* |
| | Monteria,COL | 1987 | *T. urticae* |
| *Phytoseiulus persimilis** Athias-Henriot | NET (lab colony) | 1988 & 1990 | *T. urticae* |
| *Propioseiopsis cannaensis* | CIAT, COL | 1990 | *T. urticae* (+pollen+honey) |
| *Typhlodromalus aripo* DeLeon | CIAT, COL | – | not cultured |
| *Typhlodromalus limonicus* s.l. (Garman & McGregor) | Cruz das Almas, BRA | Mar. 1989 | *M.caribbeanae* |
| | CIAT, COL | – | not cultured |
| | Pivijay, COL | Apr. 1990 | *M. caribbeanae* |
| | San Juan de Betulia, COL | Sept. 1990 | *M. caribbeanae* |
| | Tacarigua, TRI | Jan. 1990 | *M. caribbeanae* |
| | Sta Isabel, VEN | Mar. 1990 | *M. caribbeanae* |
| *Typhlodromalus limonicus* s.s. | Jaguariuna, BRA<br>Riverside, USA* (lab colony) | June 1990<br>Mar. 1989 | *M. caribbeanae* and *T. urticae* |
| *Typhlodromalus tenuiscutus* | Los Cordobas, COL | Febr. 1990 | *M. caribbeanae* |
| | Quevedo, ECU | June 1990 | *M. caribbeanae* |

* Not reported on cassava

BRA=Brazil; COL=Colombia; ECU=Ecuador; MEX=Mexico; NET=Netherlands; TRI=Trinidad; VEN=Venezuela obtained from detached leaf cultures according to Bellotti *et al.* (1987). Egg cohorts were produced by adding fresh, infested cassava leaves to the cultures and collecting the eggs laid on these leaves within 24 hours. Field collected females of *T. limonicus* and *T. aripo* were put individually in small plastic containers (2 $cm^3$) on a cassava leaf disc infested with *M. tanajoa*. The eggs were removed for use in experiments within 24 hours. The spider mite species tested were: *Mononychellus caribbeanae*, *M. mcgregori* Flechtman and Baker, *M. tanajoa*, *Oligonychus gossypii*, *O. peruvianus* and *Tetranychus urticae*. Tetranychids were reared on potted young cassava plants. To obtain cohorts of eggs, females were transferred to clean detached cassava leaves. Eggs were collected the following day.

Humidity chambers were constructed from small plastic boxes. A circular hole was cut in the lid with a diameter adjusted to exactly fit the size of the hygrometer probe (Cole-Palmer LCD model 3309-50). The hole was closed during the experiments. All box seams were sealed with both vaseline and parafilm. Constant predefined humidities were created by using salt solutions in distilled water (Winston and Bates, 1960). All chemicals were analytical grade. With the exception of $CaNO_3$ and $MgCl_2$, solutions were supersaturated. $CaNO_3$ and $MgCl_2$ were diluted until the solutions produced the humidity desired for the experiments (see Table 2). Relative humidities were measured immediately before and after the experiments. Readings were taken after at least 30 minutes of incubation. Care was taken to minimize disturbance to the air layer above the solution. The solutions did not produce the humidities reported by Winston and Bates (1960), however they were constant throughout the experiments, even with the non-saturated solutions (Table 2).

The eggs were carefully placed on a microscope slide with a camel's hair brush. For the phytoseiids, 30 eggs of two species/strains each were placed per slide. Five slides were placed together in one humidity chamber on a small perforated plat-

TABLE 2

Salt solutions with corresponding relative and absolute humidities. Readings were taken at 25 °C; *n* is the number of recordings.

| Solutions | Relative humidity (%) | Saturation deficit (mmHg)[a] | *n* |
|---|---|---|---|
| $H_2O$ (distilled) | 100%[b] | 0 | - |
| $KNO_3$ | 91.0% ± 2.1% | 2.14 | 9 |
| KCl | 83.4% ± 1.7% | 3.94 | 10 |
| NaCl | 75.7% ± 1.3% | 5.77 | 12 |
| $CaNO_3$[c] | 66.1% ± 0.8% | 8.97 | 10 |
| $MgCl_2$[c] | 53.5% ± 2.0% | 11.05 | 3 |
| NaI | 38.0% ± 1.4% | 14.73 | 5 |
| $CaCl_2$ | 24.3% ± 2.1% | 17.99 | 2 |

[a] Saturation vapor pressure at 25°C taken as 23.76 mmHg.
[b] By estimation (not in hygrometer range).
[c] Solution not saturated.

form ca. 1 cm above the solution. Species/strains combinations were randomized on each slide throughout the experiments. For the tetranychids, 75 eggs of one species were placed per slide. This higher number was chosen to compensate for the expected higher overall mortality. The humidity chambers were placed in a temperature-controlled climate chamber at 25 ± 1°C.

### *Metereological data*

The exact original collection site of all phytoseiids tested was known. Metereological data of these sites were obtained from CIAT's database using the GIS coordinate system. In all cases the data were obtained by interpolating between the four closest wheather stations. Only long term averages were used for the analyses with a minimum record of five years. The following data were used: annual rainfall, number of dry months per year, temperature, relative humidity and dewpoint. A complete record was available only for the first three parameters. When relative humidity data were available, vapour pressure deficits were calculated using this parameter and the maximum vapour pressure at the average annual temperature. If only dewpoint was known the deficit was calculated using the maximum vapour pressure at the average annual temperature and at the dewpoint.

### *Statistical analysis*

All relative humidities measured were converted to the more appropiate standard of saturation deficit (*cf.* Ferro and Chapman, 1979). Subsequently, the percentage of egg hatch recorded under each condition was plotted against the saturation deficit. In this way the shape of the response curves could be defined. To further analyse the data for the phytoseiids and to compute $SD_{50}$-values, probit analysis was applied according to Finney (1971). This was done by means of a customized computer programme (Robota Software). Weighted linear regression was applied to determine parallelism of the response curves obtained. Relationships between $SD_{50}$ and metereological data were studied using (stepwise) multiple regression. Finally, the most important outcomes of the regression analysis were confirmed with the non-parametric Spearman's rank correlation test.

## RESULTS

Both the phytoseiids and the tetranychids show markedly congruent response curves (Figs 1a and b). However, this within-family similarity contrasts with the differences observed between them. First, whereas all phytoseiids show a sigmoid response to increasing saturation deficits with no egg mortality occurring when there is no deficit, the tetranychid response can be characterized as trapezoid with considerable egg mortality when humidity is high. Moreover, whereas the transition from low to high egg mortality is very steep for the phytoseiids, it is much more gradual in the tetranychids. Thus, in a certain humidity domain the phytoseiids are much more susceptible to small changes in the saturation deficit than are

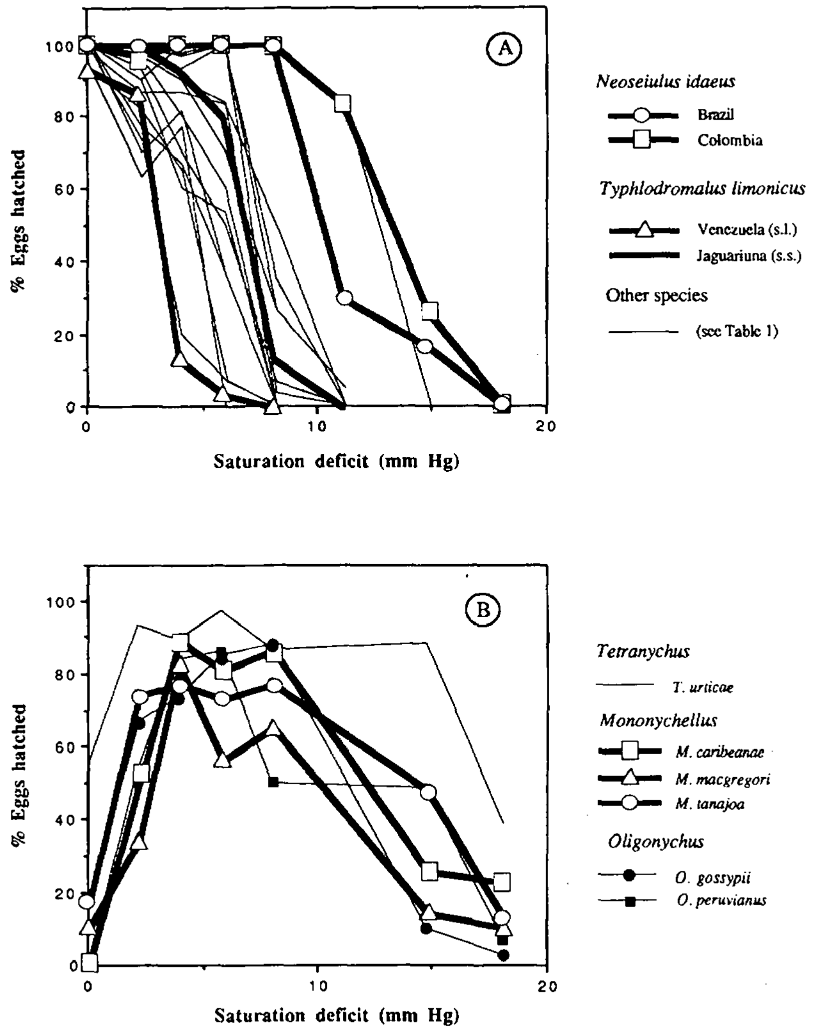

Fig. 1. Response (percent egg hatch) to increasing saturation deficits for A) all phytoseiids tested and B) all tetranychids tested. Note that phytoseiids show a sigmoid response, whereas tetranychids have a trapezoid response curve.

the tetranychids. Additionally, there appear to be marked interspecific and interstrain differences in the location of the response curve for the phytoseiids, but not for the tetranychids. The latter differ in the magnitude of their response, but not in relative changes in egg hatch with changing saturation deficits. This implies that the various tetranychid species tested tolerate the same range of saturation deficits, whereas there are significant differences in this respect among the phytoseiids. With the exception of *N. idaeus* and *P. persimilis*, the eggs of the predaceous mites tested were much more susceptible to high saturation deficits than those of the spider mites. This corroborates the hypothesis that the observed differences in seasonal abundance between phytophagous cassava mites and their predators is related to a different saturation deficit tolerance spectrum of the eggs.

Probit analysis was applied to analyse the similarity seen in the slopes of the response curves for the phytoseiids (Fig. 1a) and to compute the saturation deficit at which 50% of the eggs no longer hatch ($SD_{50}$). Weighted linear regression showed that the various slopes were not significantly different, with the exception of *T. aripo*. This implies that the tolerance of the species/strains tested can be compared in terms of their $SD_{50}$. It appears that between-strain differences in $SD_{50}$-values for the *T. limonicus s.l.* group (*e.g.* between the Venezuela and the CIAT strain) may be larger than some of the interspecific differences (Table 3).

Climate data for the collection sites are given in Table 4 together with $RH_{50}$ values. The latter are the 25 °C equivalents of the $SD_{50}$-values given in Table 3. Stepwise multiple regression involving all parameters given in Table 4 showed that the only reliable predictor of $SD_{50}$ (or $RH_{50}$) is average relative humidity (ARH). A regression model with only $SD_{50}$ and ARH showed the association to be strong ($P$=0.003; $R^2$=0.579, $n$=11). This result was confirmed by Spearman's test ($P$=0.012). Significant relationships could not be obtained for any of the other factors.

## DISCUSSION

The suppression of tetranychid pests by phytoseiid predators may critically depend on ambient humidity as was demonstrated by Stenseth (1979). He showed that the two spotted spider mite, *Tetranychus urticae,* was effectively controlled by *Phytoseiulus persimilis* at 27°C with RH between 60 and 90%, but found no impact of the predator at the same temperature when relative humidity was 40%. At 40% RH none (this paper) or only 7.5% of the eggs of *P. persimilis* (Sabelis, 1981, see also Begliarow, 1967) are able to hatch, whereas this RH has no effect on the viability of the eggs of the spider mites (Ferro and Chapman, 1979). Kramer and Hain (1989) observed that variable humidity and temperature regimes had no significant effect on survival of immature stages of the spruce spider mite, *Oligonychus ununguis* (Jacobi), while survival of the predatory mite *Neoseiulus fallacis* (Garman) was strongly reduced by recurrent high saturation deficits. They concluded that the meteorological conditions in the field during hot, dry summer months may not support a large population of *N. fallacis* and thereby allow the build-up of populations of the spruce spider mite. In the Spanish citrus belt, populations of *Euseius stipulatus* (Athias-Henriot) decline despite the presence of abundant prey. This is also attributed to the combination of high temperatures and high saturation deficits during the summer (Ferragut et al. 1987). In contrast to its prey, no eggs of *E. stipulatus* hatched at relative humidities below 60%. In addition to the exclusion of their natural enemies, spider mites are also directly favoured by high saturation deficits

TABLE 3

Regression equations obtained by probit analysis on egg hatch data at various saturation deficits (mmHg). Also given are the saturation deficits at which 50% of the eggs do not hatch ($SD_{50}$) with 95% confidence limits. Ranking is according to $SD_{50}$. For abbreviated country codes see Table (1).

| Species tested | Strain | Slope | Variance | Y-intercept | SD50 | Confidence limits (95%) | |
|---|---|---|---|---|---|---|---|
| | | | | | | Upper | Lower |
| *T. limonicus s.l.* | Valera, VEN | 0.70 | 0.011 | 2.97 | 2.92 | 2.05 | 3.78 |
| *T. tenuiscutus* | Quevedo, ECU | 0.55 | 0.006 | 3.30 | 3.09 | 2.59 | 3.60 |
| *T. tenuiscutus* | Los Córdobas, COL | 0.50 | 0.005 | 3.40 | 3.21 | 2.68 | 3.74 |
| *T. limonicus s.l.* | Cruz das Almas, BRA | 0.56 | 0.006 | 3.03 | 3.54 | 2.43 | 4.66 |
| *T. limonicus s.l.* | Pivijay, COL | 0.47 | 0.004 | 2.89 | 4.51 | 3.96 | 5.06 |
| *T. limonicus s.l.* | San Juan de Betulia, COL | 0.45 | 0.004 | 2.77 | 4.92 | 3.65 | 6.20 |
| *P. macropilis* | Recife, BRA | 0.49 | 0.005 | 2.55 | 4.97 | 3.91 | 6.02 |
| *P. macropilis* | Monteria, COL | 0.49 | 0.005 | 2.41 | 5.33 | 4.77 | 5.89 |
| *T. limonicus s.l.* | Tacarigua, TRI | 0.62 | 0.008 | 1.54 | 5.55 | 5.07 | 6.04 |
| *T. limonicus s.s.* | Riverside, USA | 0.68 | 0.010 | 0.83 | 6.17 | 5.04 | 7.31 |
| *C. pilosa* | Pico de Oro, MEX | 0.66 | 0.007 | 0.81 | 6.37 | 3.97 | 8.78 |
| *T. limonicus s.s.* | Jaguariuna, BRA | 0.71 | 0.009 | 0.34 | 6.58 | 6.17 | 6.98 |
| *T. limonicus s.l.* | CIAT, COL | 0.46 | 0.009 | 1.86 | 6.81 | 6.12 | 7.49 |
| *N. californicus* | Bogotá, COL | 0.60 | 0.010 | 0.62 | 7.32 | 6.79 | 7.85 |
| *T. aripo* | CIAT, COL | 0.29 | 0.002 | 2.76 | 7.83 | 6.88 | 8.78 |
| *P. cannaensis* | CIAT, COL | 0.50 | 0.006 | 0.73 | 8.62 | 7.43 | 9.81 |
| *P. persimilis* | NET | 0.52 | 0.006 | 0.33 | 8.95 | 5.66 | 12.23 |
| *N. idaeus* | Petrolina, BRA | 0.42 | 0.003 | 0.21 | 11.29 | 9.94 | 12.65 |
| *N. idaeus* | Fonseca, COL | 0.49 | 0.006 | -1.52 | 13.25 | 12.54 | 13.96 |

because feeding rate is increased to compensate for the loss of water by evaporation through the cuticle at low atmospheric humidity (Wharton and Richards, 1978). Hence, dry conditions will favour tetranychid population growth, because food intake rate (and thus mass conversion) will be higher.

A number of laboratory studies have shown that high saturation deficits generally have a much stronger impact on the predator than on the prey. It has been repeatedly demonstrated that for tetranychid eggs only very low and very high humidities cause egg mortality (*e.g.* Boudreaux, 1958; Nickel, 1960; Harrison and Smith, 1961; McEnroe, 1963; Hazan *et al.*, 1973; Ferro and Chapman, 1979; Sabelis, 1981; Perring *et al.*,1984; this study). For Phytoseiidae on the other hand most studies show a high sensitivity for moderate to high deficits, but not for low deficits. Dinh *et al.* (1988) provide several examples of studies where hatching success of phytoseiid eggs was very poor below 50% RH (at ± 25°C). For the majority of the species/strains studied in this paper, 85% of the eggs died at relative humidities of 65%-80%. Because the feeding stages can, to a certain extent, compensate for water loss by the uptake of free water or food (*cf.* Mori and Chant, 1966b; Swift and Blaustein, 1980; Dinh *et al.*, 1988) or even by the uptake of water vapour from the atmosphere (Gaede, 1992), eggs are most vulnerable to dehydra-

TABLE 4

Metereological data concerning the collection sites of the populations used for the experiments. All data are long term averages, with a minimum record of five years. For calculation of VPD see text. Also given are relative humidities at which 50% of the eggs no longer hatch (calculated from Table 3 for 25•C).

| Species tested | Strain | RH50 | AAR (25°C) | DMY (mm) | T (°C) | ARH (%) | DP (•C) | VPD | ALT (m) (mm Hg) |
|---|---|---|---|---|---|---|---|---|---|
| *T. limonicus s.l.* | Valera, VEN | 87.7 | 916 | 3 | 26 | 77 | 5.81 | 153 | |
| *T. tenuiscutus* | Quevedo, ECU | 87.0 | 2158 | 6 | 24 | 85 | 22 | 3.36 | 104 |
| *T. tenuiscutus* | Los Córdobas, COL | 86.5 | 1242 | 4 | 28 | 80 | 21 | 5.68 | 280 |
| *T. limonicus s.l.* | Cruz das Almas, BRA | 85.1 | 1160 | 2 | 23 | | | | 225 |
| *T. limonicus s.l.* | Pivijay, COL | 81.0 | 1316 | 4 | 27 | 80 | | 5.35 | 300 |
| *T. limonicus s.l.* | San Juan de Betulia, COL | 79.3 | 988 | 4 | 26 | | | | 225 |
| *P. macropilis* | Recife, BRA | 79.1 | 1667 | 3 | 26 | 75 | 23 | 6.31 | |
| *P. macropilis* | Monteria, COL | 77.6 | 1133 | 4 | 28 | 80 | | 5.68 | 20 |
| *T. limonicus s.l.* | Tacarigua, TRI | 76.6 | 1577 | 4 | 26 | | 24 | 2.84 | 43 |
| *T. limonicus s.s.* | Riverside, USA | 74.0 | | | | | | | |
| *C. pilosa* | Pico de Oro, MEX | 73.2 | 2175 | 1 | 28 | 80 | | 5.68 | |
| *T. limonicus s.s.* | Jaguariuna, BRA | 72.3 | 1241 | 6 | 20 | | | | |
| *T. limonicus s.l.* | CIAT, COL | 71.3 | 1055 | 2 | 24 | 72 | 18 | 6.27 | 1060 |
| *N. californicus* | Bogotá, COL | 69.2 | 1048 | 2 | 14 | 70 | 10 | 3.60 | 3200 |
| *T. aripo* | CIAT, COL | 67.0 | 1055 | 2 | 24 | 72 | 18 | 6.27 | 1060 |
| *P. cannaensis* | CIAT, COL | 63.7 | 1055 | 2 | 24 | 72 | 18 | 6.27 | 1060 |
| *P. persimilis* | NET | 62.3 | | | | | | | |
| *N. idaeus* | Petrolina, BRA | 52.5 | 425 | 8 | 25 | | 20 | 6.23 | 230 |
| *N. idaeus* | Fonseca, COL | 44.2 | 946 | 5 | 29 | | | | 180 |

Legend: AAR = average annual rainfall; DMY = number of dry months per year; T = average annual temperature; ARH= average relative humidity; DP = dewpoint; VPD = vapour pressure deficit; ALT = altitude. For abbreviation of country codes see Table 1.

tion. Zhang and Kong (1985) reached the same conclusion by comparing survival of eggs and larvae at low humidities.

Although the qualitative differences in the humidity tolerance spectrum between the two families found in laboratory studies will remain, care should be taken in extrapolating these findings to the field situation. First, ambient humidity may not be a suitable measure for the field. Most tetranychids and phytoseiids oviposit on the lower leaf surface, where they also spend most of their time. Because of their very small size (generally < 500μm) they will experience the conditions in the leaf boundary layer rather than the ambient conditions. Absolute humidities in the phylloplane may differ from those in the ambient air (see *e.g.* data provided in Gaede, 1992). This will depend on *e.g.* plant morphology, plant physiology and presence of spider mite web and faeces (Hazan *et al.*, 1973). Ferro and Southwick (1984) provide a model for calculating humidity in the unstirred laminar leaf boundary layer when leaf-, nearby air-temperature, and relative humidity of ambient air are known. They also show, however, that when wind speed exceeds 0.1 m/s, humidity within the canopy will give a close approximation of humidity close to the leaf surface. Secondly, as shown by Gaede (1992), Penman and Chapman (1980), and Mori and Chant (1966b) both predator and prey can exhibit a behavioural response to changing humidities. This implies they must be able to somehow measure the humidity in their direct environment. If so, the mobile stages not only can avoid dehydration via drinking or feeding but are also able to reduce the risk by searching for more favourable sites. Moreover, females can deposit their eggs in more sheltered places (Swift and Blaustein, 1980). Many plant species are known to provide (predatory) mites with domatia (*e.g.* Pemberton and Turner, 1989; O'Dowd and Wilson, 1989,1991; Walter and O'Dowd, 1992). Without doubt these domatia will protect the mites and especially their eggs against desiccation, which may well be their single most important function. Thirdly, most laboratory studies are done under conditions of constant humidity, whereas in nature humidity follows a diurnal cycle, being highest at night and lowest during the day. At night, when humidity approaches saturation, radiative cooling of the leaf frequently brings about condensation on the leaf surface (Burrage, 1971). Thus, even in drier areas, humid conditions occur during certain periods of the day. Little is known, however, about the time-span during which the phytoseiids can tolerate dry conditions. Kramer and Hain (1989) showed that *N. fallacis* can survive when stressed for relatively short (one-third of a day) periods of time. Gaede (1992) demonstrated that *P. persimilis* females compensated previously suffered deficits within a "few hours" by active uptake of water vapour at relative humidities of 90% and above at 15–25 °C. Zhang and Kong (1985) reached a similar conclusion for the eggs of *N. fallacis*. They found an increase in hatch success when eggs were transferred from a low humidity regime to a high humidity regime during the last few hours of the egg stage.

Our results (and those obtained by several other authors) show that response curves for phytoseiid eggs have a narrow humidity domain where hatch success declines from 100% to 0%, indicated by slope and variance of the probit regression line. Moreover, the data obtained with *T. limonicus* s.l. indicate that, at least for this species, the position of the switchpoint (characterized by the $SD_{50}$) is a strain-specific character. Clearly, too few strains were tested of the other species to generalize this statement. Nevertheless, the question emerging from these observations is why the tolerance spectrum in some phytoseiids is broad, whereas in others it is narrow, for it is in the absence of a cost factor that one would expect natural selection to favour strains/species with a broad tolerance spectrum. Thus, the variation observed implies that the benefit of being tolerant to a wide range of saturation deficits is offset by some cost factor.

That $SD_{50}$-values were strongly correlated with average relative humidity and not with vapour pressure deficit (VPD) seems surprising as it is the absolute humidity that determines the water balance. However, there are two reasons why in this case RH is more accurate than VPD. First, VPD was calculated using a combination of data, all of which were subject to measurement error. The inaccuracy of VPD is most obvious when comparing values obtained using RH with values obtained using dewpoint data whenever both are available. Large discrepancies also arise when comparing measured RH-values with RH-values calculated using dewpoint data. Second, with the exception of *Neoseiulus californicus* from Bogota, all populations used for the analysis were obtained from regions within a narrow temperature domain (25.9 ± 1.8 °C). Under these conditions RH is a good approximation of VPD. Thus our statistical analysis showed that much of the between strain/species variation can be explained by variation in average relative humidity of the collection locality. This indicates that the position of the SD50 is tuned to local circumstances and hence that there is strong selection on this trait.

Assuming that the tolerance spectra determined with eggs are indicative for the tolerance of the mobile stages as well, we hypothesize that the cost involved in being tolerant to high saturation deficits is expressed as reduced competitive ability under less stressful conditions. Dunson and Travis (1992) provide several examples indicating that species capable of coping physiologically with rigorous environments are often poor competitors against ecologically similar species from (and in) less stressful habitats. Considering the experimental results obtained by Mangini and Hain (1991) it seems that this also applies to phytoseiid mites and their saturation deficit tolerance spectrum. These authors found that at low VPD *N. fallacis* was the better competitor, whereas a high VPD favoured *M. occidentalis*. Given that competition between phytoseiids may be quite strong (*cf.* Strong *et al.*, 1984) reduced competitive ability as a cost factor may well explain the strain specificity of SD50-values as found in this study. Moreover, the distribution of cassava inhabiting phytoseiids in both time and space also points at a cost factor involved in being tolerant to saturation deficits. In the humid parts of Northeast Brazil *T. limonicus* may not be present on the crop when its prey is most abundant, *i.e.* in the dry season (Noronha and Moraes, 1989). Furthermore it appears that the SD-tolerant *N. idaeus* is the predominant species on cassava in the dry parts of Northeast Brazil and the dry Guajira region of Colombia and coastal Venezuela, whereas the generally susceptible *T. limonicus* is found in a much wider range of habitats, *viz.* from the tropical rain forest to seasonally dry areas.

When testing the hypothesis that enhanced tolerance to saturation deficits coincides with reduced competitive ability one would also be interested in the underlying mechanism. As the water balance is determined by processes governing water gain (feeding, sorption) and water loss (defecation, transpiration), it follows that physiological mechanisms restricting water loss will also restrict water gain and thus feeding rates. Although this hypothesis as such has not been tested, it is clear from the literature that both feeding and oviposition rates for certain species decrease with decreasing VPD's (*e.g.* Fournier *et al.*, 1985; Swift and Blaustein, 1980; Pralavorio and Almaguel-Rojas, 1979; Mori and Chant, 1966a). It can therefore be hypothesized that, under conditions of low VPD, species/strains with a low level of tolerance (low SD50) will have higher feeding (and thus oviposition) rates than species/strains with a high SD50. When co-occurring, tolerant individuals would therefore be at a competitive disadvantage under humid conditions because the resource is exploited at a higher rate by the susceptible ones.

The outcome of this study has consequences for the selection of phytoseiid natural enemies for biological control purposes. The most important finding is that the humidity tolerance spectrum can be extremely narrow. Moreover, it was demonstrated that, at least for *T. limonicus*, the tolerance level is not a species-specific trait but rather a strain-specific trait determined by climatological characteristics of the habitat. This illustrates the importance of looking for natural enemies in zones that match the climate in the area where the natural enemies are needed. The climate matching principle is one of the cornerstones of IITA's programme for biological control of the cassava green mite (see *e.g.* Yaninek and Bellotti, 1987).

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