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HOW QUALITY OF HOST PLANT AFFECTS A PREDATOR–PREY INTERACTION IN BIOLOGICAL CONTROL¹

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Abstract. In cases of successful biological control the pest population is maintained at low densities by a natural enemy, but the mechanisms by which the predator or parasitoid manages to control the pest are often unknown. This study was undertaken to determine the response of a predator to different population growth rates of its prey within a biological control system. Population growth rate of the phytophagous mite *Panonychus ulmi* was varied by altering the nutritional status of the host plant (apple trees [*Pyrus malus*]). NPK fertilizer was added to the soil, resulting in higher nitrogen, lower phosphorus, and lower potassium levels in the foliage of the trees. There appeared to be a nonlinear relationship between nitrogen and *P. ulmi* densities, with density increasing and then decreasing as nitrogen concentration was increased. Two predaceous mites, *Typhlodromus pyri* and *Zetzellia mali*, were implicated in the control of *P. ulmi*, but the effectiveness of both was reduced at high nitrogen levels. The predators therefore did not fully compensate for increases in the population growth rate of their prey, although *P. ulmi* densities were maintained well below the economic threshold in all cases. However, the probability of persistence of the prey populations was not significantly affected by the nutrient regimes, suggesting that the fundamental dynamics of the predator–prey interaction were not altered by the range of population growth rates in this study.

Key words: Acari; biological control; numerical response; *Panonychus ulmi*; plant nutrition; population dynamics; predator–prey; *Typhlodromus pyri*.

INTRODUCTION

In successful biological control, a pest population is maintained at low densities by its natural enemies, but it is often not clear by what mechanism(s) the predator or parasitoid attains that control. The relative contribution of processes that occurs within populations (aggregation, functional and numerical responses) vs. processes that occur among populations (migration) to successful biological control has been much debated (Waage and Hassell 1984, Murdoch et al. 1985, Taylor 1990, 1991). In recent work with phytophagous and predaceous mites on apple trees (Walde 1991, 1994, and *in press*), I showed that interpopulation processes did affect prey densities, and that higher levels of prey migration could increase the time that prey populations persist. In addition, I also suggested that the fundamental dynamics (eventual extinction of the prey population) were driven by processes operating within the population, principally by characteristics of the predator–prey interaction. A key to unraveling these dynamics is to understand the nature of the numerical response of the predator to differences in the density of its prey. Here I describe an experiment aimed at looking at predator response under conditions that lead to different rates of population growth in the prey. I make use of the fact that this predator–prey interaction

occurs on plants, which are an interactive part of the system.

Empirical studies of the biological control of arthropod pests have typically focussed on the behavior and ecology of the pest and natural enemy, while other predators, other prey, and the host plant have been considered part of a non-interactive environment. This is beginning to change, as the importance of interactions among the three trophic levels, plant, herbivore, and natural enemy, has been recognized (e.g., Price et al. 1980), and studies of tri-trophic interactions have become more common for natural ecosystems (Lettourneau 1988). The potential impact of the host plant on predator–prey interactions has also begun to attract attention in studies of biological control in agriculture and forestry (e.g., Dicke and Sabelis 1992, Hare 1992). One general way in which the quality of the host plant may determine the effectiveness of natural enemy control is by altering the population growth rate of the herbivore via effects on fecundity, survivorship, and development rate. Changes in herbivore population growth rate can affect control by natural enemies by changing the abundance, renewal rate, and age or size structure of the herbivore population. For example, reductions in herbivore development rate have been shown to lead to increased (Loader and Damman 1991) or decreased (Clancy and Price 1987) vulnerability to natural enemies, and higher rates of increase due to changes in fecundity or survivorship can reduce the impact of natural enemies (Hanks and Denno 1993).

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Many aspects of the chemistry and physical structure of the host plant can affect population growth rates of herbivores, but one of the more important aspects, and certainly the most studied nutritional component, is nitrogen content. Increasing nitrogen content, or nitrogen mobilization, appears to be beneficial to many phytophagous insects and mites, often increasing fecundity, development rate, or survivorship (McNeill and Southwood 1978, Mattson 1980, White 1984, Rodriguez and Rodriguez 1987, Wermelinger et al. 1991, and references within).

Panonychus ulmi (Acari: Tetranychidae) is a widespread pest of apple trees that feeds on leaf tissue. The mites puncture the epidermis of the leaf with their stylets, penetrate the parenchyma, and ingest the cell contents (Kuenen 1948). It has been shown in laboratory cultures (Rodriguez 1958, Breukel and Post 1959, Rodriguez and Campbell 1961) and greenhouses or nurseries (Rodriguez 1958, Breukel and Post 1959, van de Vrie and Boersma 1970, van de Vrie and Delver 1979) that leaves containing higher levels of nitrogen host higher densities of *P. ulmi*, and that this increase in abundance is mostly due to increased egg production by mature females (Kuenen 1948, Breukel and Post 1959, van de Vrie and Boersma 1970).

Under relatively benign pesticide regimes, *P. ulmi* can be kept at low densities by the predaceous mite *Typhlodromus pyri* (Acari: Phytoseiidae). Past studies on the effect of nitrogen levels on *P. ulmi* populations in the presence of their natural enemies have led to somewhat contradictory conclusions. Post (1962) found that higher nitrogen levels significantly increased *P. ulmi* densities under field conditions. Lord and Stewart (1961), on the other hand, concluded that adding fertilizer to apple trees had no effect on field populations of *P. ulmi* when the predator populations were undisturbed. In a glasshouse experiment Van de Vrie and Boersma (1970) found that the augmentative effect of nitrogen on *P. ulmi* was considerably reduced in the presence of a phytoseiid predator.

The effect on the herbivore–predator interaction of altering host plant quality will be determined largely by the functional and numerical responses of the predator to the altered growth rate of its prey. If the predator has a sufficiently strong response, it can potentially compensate for the increased growth rate of the prey, and little or no change in prey density will be seen. Correlations between *P. ulmi* and the predator *T. pyri* at the spatial scale of a tree (Nyrop 1988, Walde 1991) suggest that *T. pyri* is able to respond numerically to increased *P. ulmi* densities under field conditions. The increased oviposition rate of *P. ulmi* in response to elevated foliar nitrogen levels thus provides an opportunity to look at the numerical response of *T. pyri* to prey populations growing at different rates.

The predator–prey interaction that is not impacted to some degree by interactions with other species under field conditions is probably the exception in biological

control. In apple orchards, other species of predaceous and phytophagous mites are commonly present, and among the most abundant are *Zetzellia mali* (Acari: Stigmaeidae) and *Aculus schlechtendali* (Acari: Eriophyidae). The predatory *Z. mali* is often abundant, but it is not thought to be capable of controlling *P. ulmi* populations on its own (Santos 1976, White and Laing 1977). *A. schlechtendali* is a tiny phytophagous mite that can be quite abundant, but rarely reaches pest levels in the study area. It is consumed by both *T. pyri* and *Z. mali*.

Here I test the hypothesis that the predator *T. pyri* is able to compensate for increases in *P. ulmi* population growth rate caused by increased nitrogen supply to the host plant under field conditions, where other potentially interacting species are present. I also begin to address the larger question of whether we need to consider the nutritional status of the host plant in interpreting predator–prey interactions in biological control.

STUDY ORGANISMS

Panonychus ulmi is a widespread pest of apple and other deciduous trees, and at high densities reduces the photosynthetic activity of leaves (Mobley and Marini 1990), which can lead to lower fruit production (Hardman et al. 1985). *P. ulmi* completes 3–5 generations/yr in the study area (Herbert 1970). The first generations lay summer eggs on the leaves, while the last produces diapausing eggs that overwinter in crevices on the bark of the trees. *P. ulmi* has five principal life stages: egg, larva, protonymph, deutonymph, and adult, with each motile stage entering a quiescent, non-feeding stage prior to molting.

T. pyri is a common phytoseiid predator of *P. ulmi* in eastern Canada and the northeastern United States. It can feed on pollen and fungi as well as other mites such as *A. schlechtendali* and *Tetranychus urticae*, but behavioral and diet analyses have shown that *P. ulmi* is the preferred prey (Dicke 1988, Dicke and DeJong 1988, Nyrop 1988). *T. pyri* consumes larval, protonymph, deutonymph, and adult stages of *P. ulmi* but does not feed on the egg stage (Walde et al. 1992). Both *T. pyri* and *P. ulmi* disperse among leaves within trees by crawling, and among trees within an orchard by wind. Neither species appears to move to ground vegetation, either for dispersal or for feeding.

Z. mali is also a common generalist predator in apple orchards. It consumes *P. ulmi* and *A. schlechtendali*, as well as pollen and plant tissue, but prefers *A. schlechtendali* (Magagula 1993). In contrast to *T. pyri*, *Z. mali* preferentially consumes eggs of *P. ulmi* in comparison to other life stages (Clements and Harmsen 1990). *Z. mali* is far more sedentary than *T. pyri*; under field conditions, residence time on a leaf is over three times as long for *Z. mali* as for *T. pyri* (Lawson and Walde 1993).

Although *A. schlechtendali* is found in all apple

growing regions of North America, Europe and Australia, it rarely becomes a significant pest and thus has not been extensively studied. There appear to be three generations per year in the study area (Herbert 1974). Adult females overwinter in hibernation sites on the bark, moving to the new green tissue at bud burst (Easterbrook 1979), and can thus be present in significant numbers earlier in the season than motile stages of *P. ulmi*.

METHODS

Experimental manipulations were carried out in a 3-yr-old Nova-Mac apple orchard, where trees were arranged in 6 blocks of 20 to 24 trees, and the blocks separated by ≥ 12 m. Rows were 8 m apart, and trees (≈ 1.5 m in height) were spaced at 3 m within rows. Ground cover between trees was pasture, which was mowed twice per season. Four plots were designated within each block. Each plot contained four trees (2×2), and was located at the corner of a block. Four treatments were randomly assigned to the four plots within each block, with each plot receiving one of the following: (1) natural densities of *P. ulmi*, no fertilizer; (2) *P. ulmi* densities augmented, no fertilizer; (3) *P. ulmi* densities augmented, 1 kg fertilizer per tree; (4) *P. ulmi* densities augmented, 2 kg fertilizer per tree. Buffer trees between the plots were unmanipulated. Experimental treatments (fertilizer application and *P. ulmi* augmentation) were set up each year in late spring (27 May to 8 June); treatments were assigned to the same plots in both years. For the fertilizer treatments, a commercial dry mix of 20:5:5 NPK was spread by hand to the edge of the canopy of the trees once each spring. It was necessary to augment densities of *P. ulmi* to test for a numerical response by the predators since natural densities were extremely low. *P. ulmi* was introduced by attaching infested apple leaves obtained from another orchard to the experimental trees and allowing the mites to move onto the living foliage. The leaves attached to each tree contained an average of 27 motile stage mites in 1991 (3 leaves with an average of 9 ± 5.6 mites each (mean ± 1 SD) and 60 motile stages in 1992 (9 leaves with an average of 6.7 ± 3.5 mites each to each tree. Natural enemies (*Typhlodromus pyri* and *Zetzellia mali*) were at very low densities in this source orchard and were not found on the collected leaves. Both predators were already present in the experimental orchard.

Trees were sampled for *P. ulmi* and *T. pyri* at intervals of 2–3 wk from 18 June through 3 September in 1991, and 27 May through 28 September in 1992. Ten leaves were taken randomly from each tree and examined for *P. ulmi*, *T. pyri*, and *Z. mali* (beginning 30 July 1991) under $12\times$ magnification in the laboratory. For statistical analyses, motile and quiescent larvae, protonymphs, and deutonymphs were combined into a category called juveniles. In 1992, the leaves were then brushed with a mite-brushing machine (Henderson and

McBurnie 1943), and the number of *A. schlehtendali* per tree estimated. The reliability of the brushing technique for *A. schlehtendali* was determined from a set of 35 samples where abundance was determined first by counting individuals on the leaves, then by the brushing technique. The brushing technique underestimated the number of mites present; density estimates based on brushing were 62% those of the direct counts. However, there was a tight correlation between direct and brushed counts ($r^2 = 0.985$).

In late July of each year, leaves were taken from the sample trees for nutrient analysis. In 1991, 25 leaves were taken from each tree, and leaves from trees within plots were combined for analysis. In 1992, 25 leaves were taken from each of two trees within each plot, and the analysis was performed by tree. All samples were processed by the Nova Scotia Department of Agriculture and Marketing laboratory, using a LECO Model FP28 element analyzer. Total content of nitrogen was obtained by combustion, followed by reduction of all nitrogen compounds to N_2 gas, which was then measured by thermal conductance. (It has been shown that increases in total N in apple leaves under conditions of increased nitrate supply are almost entirely due to increases in reduced nitrogen (Lee and Titus 1992).) Leaf nutrient levels are normally determined in late July by apple growers in this region, and by coinciding with this time, I could make comparisons with local standards for optimum nutrient levels. Samples were only taken once per year and thus I do not have a measure of seasonal changes in nutrient content of the leaves. However, in studies where samples were taken at more than one time of year (e.g., Mason 1958), the ranking of treatments in terms of nutrient content did not change over the season, that is, a high nitrogen tree remained a high nitrogen tree, despite seasonal changes in the concentration of nitrogen in its leaves.

Tree growth was determined by caliper measurements of stem diameter at 30 cm above the stem graft in May 1991 (prior to the first application of fertilizer) and October 1992.

An integrative measure of mite density over time, cumulative mite-days, was calculated for each tree as $\sum 0.5(N_{(x+1)} + N_x)D_{(x+1),x}$, where N_x is the number of individuals per leaf on sampling date x , and $D_{(x+1),x}$ is the number of days between sampling dates. The average number of cumulative mite-days for the four trees within each plot constituted one replicate for the analyses of variance and regressions. Plots of *P. ulmi* abundance vs. time suggested the presence of two principal cohorts in each of the two seasons (Fig. 1). One generation of *P. ulmi* was actually completed prior to the start of the experiment each year, and the deutonymphs and adults of this generation were used to augment densities. Thus although at least three generations actually occur in this area, I use the terms first and second cohort to refer to the two generations present during the experimental period. Cumulative densities were

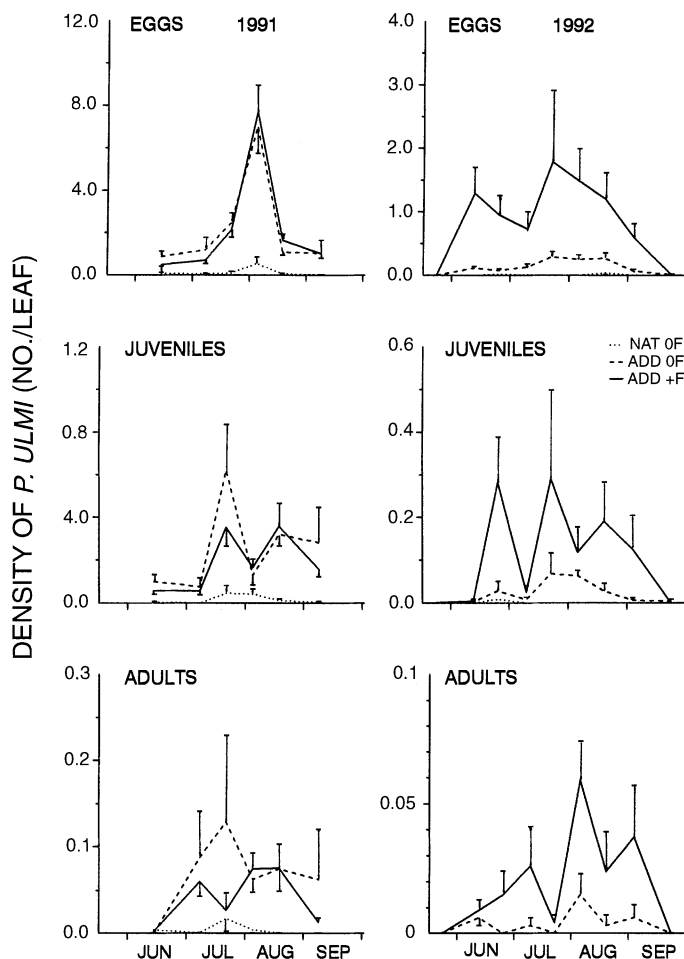


FIG. 1. Seasonal change in average density of egg, juvenile, and adult lifestages of *Panonychus ulmi* in 1991 and 1992. Experimental regimes were: (1) natural density of *P. ulmi* (NAT), no fertilizer (0F), (2) *P. ulmi* density augmented (ADD), no fertilizer, (3) *P. ulmi* density augmented, fertilizer added (+F). Densities are means of the six plots for each of the treatments and error bars are 1 SE.

calculated by cohort for the *P. ulmi* analyses, and over the whole season for the analyses of *T. pyri*, *Z. mali*, and *A. schlechtendali*. For each life stage the division between the first and second cohorts was determined as the date in July–August with the lowest density, averaged across all treatments.

Mortality, calculated as the difference of the log cumulative densities (k -value), was determined for *P. ulmi* from egg to juvenile (egg mortality) and from juvenile to adult (juvenile mortality) within each cohort. An index of egg production was obtained by dividing the cumulative number of eggs present over the season by the cumulative number of adult female *P. ulmi*.

Prior to statistical analysis, variables were tested for normality (Kolmogorov-Smirnov test) and homogeneity of variance (Bartlett's test), and log transformations were used when necessary. Differences among fertilizer treatments were determined with analysis of variance and post-hoc comparisons, and medium and high fertilizer treatments were pooled as they had nearly identical foliage nutrient levels. Results with pooled

data were not qualitatively different from unpooled analyses.

Relationships among densities, mortality, and nutrient levels were determined by multiple regression. The problem of collinearity among the nutrient variables was approached by initially determining which nutrient explained most of the variance in the dependent variable. In all cases except one (*P. ulmi* densities in the first cohort of 1991), only one nutrient (usually nitrogen) explained a significant portion of the variance, and this nutrient was then used in further analyses of species interactions.

Prey–predator ratios were calculated by summing the number of prey and number of predators observed across all samples within a treatment, and then dividing to obtain the ratio. Treatments were compared using the log-likelihood ratio contingency table test.

A crude measure of population persistence at the spatial scale of the tree was obtained for *P. ulmi* by determining the number of populations within each treatment that were still present, as determined by the presence of at least one non-zero sample from the tree

TABLE 1. Effect of fertilizer and *P. ulmi* density-augmentation treatments on macro- and micronutrient content of leaves. Values of nutrients are averages over 6 replicate plots per treatment. Treatments were 3 fertilizer levels: zero, medium, and high, and 2 density-augmentation (ADD) levels for *P. ulmi*: not augmented (0) or augmented (+). Where there were significant differences ($P < 0.05$) among treatments in the concentration of a nutrient, these are indicated by different superscript lowercase letters.

Fert. levels	ADD?	Macronutrients (% dry mass)					Micronutrients (mg/kg)				
		N	P	K	Ca	Mg	B	Fe	Mn	Cu	Zn
1991											
0	0	2.03 ^a	0.19 ^a	1.1 ^a	0.8	0.36	29	69	66	6.1	14
0	+	2.02 ^a	0.19 ^a	1.1 ^a	0.8	0.36	29	80	77	7.2	14
Med	+	2.49 ^b	0.16 ^b	1.0 ^b	0.9	0.36	28	77	82	8.4	13
High	+	2.47 ^b	0.15 ^b	0.9 ^b	0.8	0.35	27	72	72	6.5	13
1992											
0	0	1.48 ^a	0.22 ^a	1.3 ^a	0.9 ^a	0.27 ^a	34 ^a	42	67 ^a	5.6	13
0	+	1.33 ^a	0.19 ^a	1.2 ^a	0.9 ^a	0.27 ^a	33 ^a	43	77 ^a	6.6	13
Med	+	2.72 ^b	0.13 ^b	0.8 ^b	1.1 ^b	0.36 ^b	25 ^b	50	117 ^b	6.7	16
High	+	2.63 ^b	0.12 ^b	0.7 ^b	1.0 ^b	0.35 ^b	25 ^b	46	93 ^b	6.1	14

(1) on or after mid-August and (2) on or after the first of September. Winter egg laying typically begins in late August (Parent and Beaulieu 1957), and thus "disappearance" of a population prior to this suggests that it has been driven to very low levels by some factor other than the exodus of adult females to lay winter eggs. Treatments were compared using the log-likelihood ratio contingency table test. All statistical tests were conducted using SYSTAT Version 4 (Wilkinson 1988).

RESULTS

Below I first document the effect that the fertilizer treatments had on foliage nutrient levels. I then con-

TABLE 2. Average cumulative abundances (mean \pm 1 SE) for *Panonychus ulmi*, *Typhlodromus pyri*, *Zetzellia mali*, and *Aculus schlechtendali* under the fertilizer regimes.

	Life stage	Fertilizer	
		Absent	Present [‡]
<i>P. ulmi</i>			
1991 Cohort 1	Egg	92 \pm 19	89 \pm 12
	Juv	10.1 \pm 3.8	6.5 \pm 1.3
	Adult	2.9 \pm 1.5	1.3 \pm 0.4
1991 Cohort 2	Egg	79 \pm 9	93 \pm 12
	Juv	9.5 \pm 1.7	9.5 \pm 1.7
	Adult	2.4 \pm 1.0	2.0 \pm 0.5
1992 Cohort 1	Egg	3.8 \pm 1.1***	39.9 \pm 10.0
	Juv	0.5 \pm 0.3**	4.2 \pm 1.6
	Adult	0.1 \pm 0.1 [†]	0.5 \pm 0.2
1992 Cohort 2	Egg	13 \pm 3**	77 \pm 23
	Juv	2.4 \pm 0.8	10.7 \pm 4.7
	Adult	0.3 \pm 0.2 [†]	2.0 \pm 0.7
<i>T. pyri</i>			
1991		3.4 \pm 1.1	3.0 \pm 0.5
1992		9.2 \pm 2.9	11.0 \pm 2.2
<i>Z. mali</i> (1992)			
		34 \pm 12	50 \pm 13
<i>A. schlechtendali</i> (1992)			
Early		3 \pm 1***	22 \pm 2
Whole season		420 \pm 89	492 \pm 53

[†] $P < 0.10$; ** $P < 0.01$; *** $P < 0.001$ (ANOVA).

[‡] Medium and high fertilization levels combined.

sider the effect of nutrient levels and predator densities on several aspects of *P. ulmi* dynamics: density, mortality, egg production and population persistence. Finally I look at the response of two predators, *Typhlodromus pyri* and *Zetzellia mali*, to nutrient levels and prey abundance.

Foliage nutrient levels

The addition of fertilizer significantly affected levels of nitrogen, phosphorus and potassium in the leaf tissue of the apple trees in both years, but nutrient levels did not differ for medium vs. high fertilizer levels (Table 1). In 1991 trees receiving no fertilizer had an average leaf total N concentration of 2.0% of dry mass, while trees receiving medium (1 kg/tree) and high (2 kg/tree) levels had 2.5% total N. In 1992, N concentrations were 1.4% of dry mass for no fertilizer, and 2.7 and 2.6% for medium and high levels of fertilizer. Phosphorus and potassium also varied among treatments, but were lower in the fertilized treatments.

The addition of NPK fertilizer did not significantly affect tree growth over the two seasons ($P = 0.856$). Increases in diameter at 30 cm height were 2.0 ± 2.2 , 2.3 ± 1.9 , and 2.3 ± 2.0 cm (mean \pm 1 SD) for zero, medium and high levels of fertilizer, respectively.

There were negative correlations ($n = 24$) between N and P levels (1991: $r = -0.547$, $P = 0.019$, 1992: $r = -0.560$, $P = 0.004$), and between N and K levels (1991: $r = -0.520$, $P = 0.027$, 1992: $r = -0.720$, $P < 0.001$). This type of pattern has sometimes been explained as a concentration effect, whereby trees with low nitrogen content grow less, and thus have more concentrated phosphorus and potassium in their leaf tissue (Nielsen and Hogue 1985). This may be the explanation for the results of the present study; although fertilized trees did not have significantly greater stem growth than unfertilized trees, the leaves on the fertilized trees could well have been larger.

Population dynamics of *Panonychus ulmi*

I varied nutrient levels of the foliage with the objective of inducing variation in the population growth

TABLE 3. Linear relationships for the effect of leaf nutrient concentrations and predator population densities on cumulative densities of *Panonychus ulmi*, obtained by multiple regression analysis. Predators are *Zetzellia mali* and *Typhlodromus pyri*.

<i>P. ulmi</i> life stage	Independent variable	Linear regression		Full model	
		Coeff.	<i>P</i>	<i>P</i>	<i>r</i> ²
First cohort (1991)					
Eggs	N	-80.7	0.102	0.097	0.354
	P	-857.9	0.096		
	K	96.7	0.181		
Juveniles	N	-12.9	0.131	0.149	0.308
	P	-84.6	0.264		
	K	9.2	0.389		
Adults	N	-3.5	0.031	0.003	0.622
	P	-38.4	0.025		
	K	6.7	0.009		
First cohort (1992)					
Eggs	N	1.84	0.000	0.000	0.673
	<i>Z. mali</i>	-0.41	0.020		
Juveniles	N	1.47	0.002	0.002	0.718
	<i>T. pyri</i>	0.66	0.014		
	<i>Z. mali</i>	-1.29	0.046		
	N × <i>Z. mali</i>	0.53	0.068		
Adults	N	0.96	0.035	0.030	0.373
	<i>Z. mali</i>	-0.43	0.035		
Second cohort (1992)					
Eggs	K	-2.86	0.001	0.001	0.621
	<i>Z. mali</i>	-0.03	0.014		
Juveniles	K	-5.34	0.001	0.001	0.727
	<i>Z. mali</i>	-0.19	0.001		
	<i>T. pyri</i>	-0.41	0.024		
	<i>Z. m.</i> × <i>T. p.</i>	0.02	0.013		
Adults	K	-5.53	0.000	0.001	0.758
	<i>Z. mali</i>	-0.14	0.002		
	<i>T. pyri</i>	-0.29	0.040		
	<i>Z. m.</i> × <i>T. p.</i>	0.01	0.016		

rate of *P. ulmi*. Differences in population growth rate lead to corresponding differences in population density and result from variation in mortality and fecundity rates. Below I first describe how density, mortality, and egg production of *P. ulmi* were directly related to nutrient level, and in particular to concentration of nitrogen in the foliage. Secondly I describe how *P. ulmi* density and mortality were linked to predator density, and how this relationship varied with the level of nutrients in the host plant. The links between nutrient level and prey and predator abundances are all necessarily described using regression analysis. Probable cause and effect relationships are inferred, but fully delineating causal relationships will require further experimental manipulation.

Densities of *P. ulmi* were considerably higher in 1991 than in 1992 (Fig. 1). In addition, densities were much higher on trees where populations had been augmented in the spring than on trees with natural densities (236.2 vs. 14.6 mite-days in 1991, 96.7 vs. 0.9 mite-days in 1992), and thus the analyses described below were conducted using only the 18 plots with augmented *P. ulmi* densities.

Direct effects of nutrient manipulation on P. ulmi.—

Differences in nitrogen concentration of the foliage did induce differences in the density of *P. ulmi*. The relationship between density and nitrogen was somewhat complex in that it changed over time, but these temporal changes appeared to be the result of a nonlinear response of *P. ulmi* to increases in leaf nitrogen concentration.

Initially (first cohort, 1991) densities of *P. ulmi* did not differ significantly among fertilizer treatments (Fig. 1, Table 2). However, contrary to expectations, densities of adult *P. ulmi* were *negatively* correlated with both nitrogen and phosphorus in the leaves, and positively correlated with potassium levels (Table 3). Later in the season (second cohort), there were no significant relationships between density and leaf nitrogen ($P > 0.35$), although the slopes of the relationships were still negative.

In contrast, in 1992 cumulative densities of the first cohort of *P. ulmi* were lower in the no-fertilizer treatment (Table 2). Egg, juvenile and adult densities increased with leaf nitrogen concentration (Table 3). This pattern persisted for the second cohort of the season, where the most pronounced difference among treatments was seen for the egg stage ($P = 0.009$), but

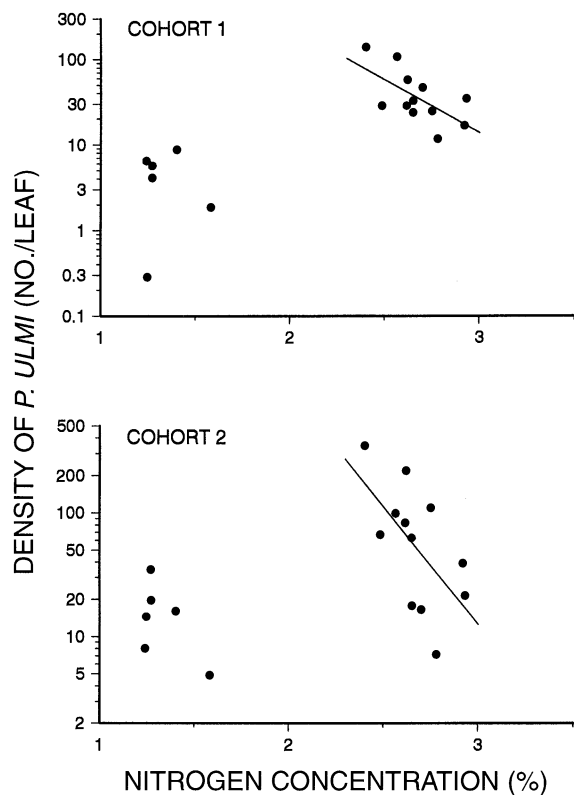


FIG. 2. Relationship between cumulative density of *Panonychus ulmi* and leaf nitrogen concentration in 1992 showing possible nonlinear response for fertilized and unfertilized plots. Regression lines are for $N \geq 2.4\%$ of leaf dry mass.

densities of juveniles and adults also tended to be higher on fertilized trees (Table 2).

The range of nitrogen concentration achieved in 1991 was narrower (1.8–2.6%) than in 1992 (1.2–2.9%). To determine if the negative relationship seen in 1991 might be part of a nonlinear relationship between *P. ulmi* and nitrogen, density of *P. ulmi* in 1992 was regressed against leaf N using only plots with relatively high ($\geq 2.4\%$) N. In both cohorts of 1992, a significantly negative relationship between density and nitrogen concentration was seen (Cohort 1: $P = 0.026$; Cohort 2: $P = 0.036$) (Fig. 2). Thus the changing patterns seen over the 4 cohorts of *P. ulmi* are likely part of one pattern, where densities increase with N concentration over the lower range of nitrogen levels, but decline at high levels of nitrogen.

Mortality (egg or juvenile) was not directly related to nitrogen level except in the second cohort of 1992, when egg mortality increased with N ($P = 0.046$) and juvenile mortality declined with N concentration ($P = 0.013$). There was no evidence of a non-linear relationship between mortality and nitrogen in any cohort.

Egg production did vary, however, with fertilizer treatment. In 1991 production of eggs was highest on trees with medium levels of fertilizer ($P = 0.032$). The

TABLE 4. Effect of nutrient regime and *Panonychus ulmi* density augmentation (ADD) on percent of populations of *P. ulmi* persisting beyond mid-August and early September. Persistence did not differ significantly among augmented populations on any date (August 1991: $P = 0.171$; September 1991: $P = 0.837$; August 1992: $P = 0.094$; September 1992: $P = 0.229$; log likelihood ratio chi-square test).

Fert.?	ADD?	1991		1992	
		Aug	Sep	Aug	Sep
No	No	29	4	9	0
No	Yes	96	50	58	29
Yes	Yes	85	56	74	49

ratios of eggs to adult females obtained for zero, medium, and high fertilizer treatments were (mean \pm 1 SE): 3.7 ± 0.3 , 4.4 ± 0.2 , and 3.7 ± 0.2 eggs per female (means \pm 1 SE). In 1992, egg production was highest on trees with the highest level of fertilizer ($P = 0.021$). Observed ratios were 3.4 ± 0.1 , 3.7 ± 0.1 , and 4.2 ± 0.3 eggs per female for zero, medium, and high levels, respectively.

Persistence of *P. ulmi* at the spatial scale of individual trees, as measured by the presence of at least one non-zero count after either mid-August or early September, was not affected by the fertilizer treatments in either year (Table 4). The proportion of populations persisting did not differ significantly among the treatments with initially augmented populations. Initial augmentation of *P. ulmi* did increase the persistence of the populations markedly.

Indirect effects of nutrients on P. ulmi: effects of predation.—Density and mortality of *P. ulmi* were also related to density of the predators *T. pyri* and *Z. mali*, particularly in 1992, and at times nutrient level played an indirect role by altering this relationship.

Neither density of *P. ulmi* ($P = 0.792$) nor egg mortality ($P = 0.147$) in the first cohort of 1991 were related to predator (*T. pyri*) density. Juvenile mortality did increase with density of *T. pyri*, but only when nitrogen levels were relatively low (Fig. 3a), i.e., there was a significant interaction between leaf N concentration and density of *T. pyri* ($P = 0.021$). Density and mortality of the second cohort of *P. ulmi* in 1991 were also unrelated to abundance of the predator *T. pyri* (density: $P = 0.369$; egg mortality: $P = 0.193$; juvenile mortality: $P = 0.937$).

In the second season, however, densities of the first cohort of *P. ulmi* were negatively related to *Z. mali* densities (Table 3). In addition, there was a suggestion that juvenile density was affected by an interaction between N levels and *Z. mali* density (Table 3), where the correlation between *Z. mali* and juvenile *P. ulmi* densities was more negative at lower nitrogen levels. In addition, high juvenile mortality was associated with high densities of *Z. mali* ($P = 0.019$) (Fig. 3c). Since high egg mortality was associated with low densities of *Z. mali* ($P = 0.014$) and *T. pyri* ($P = 0.037$), it

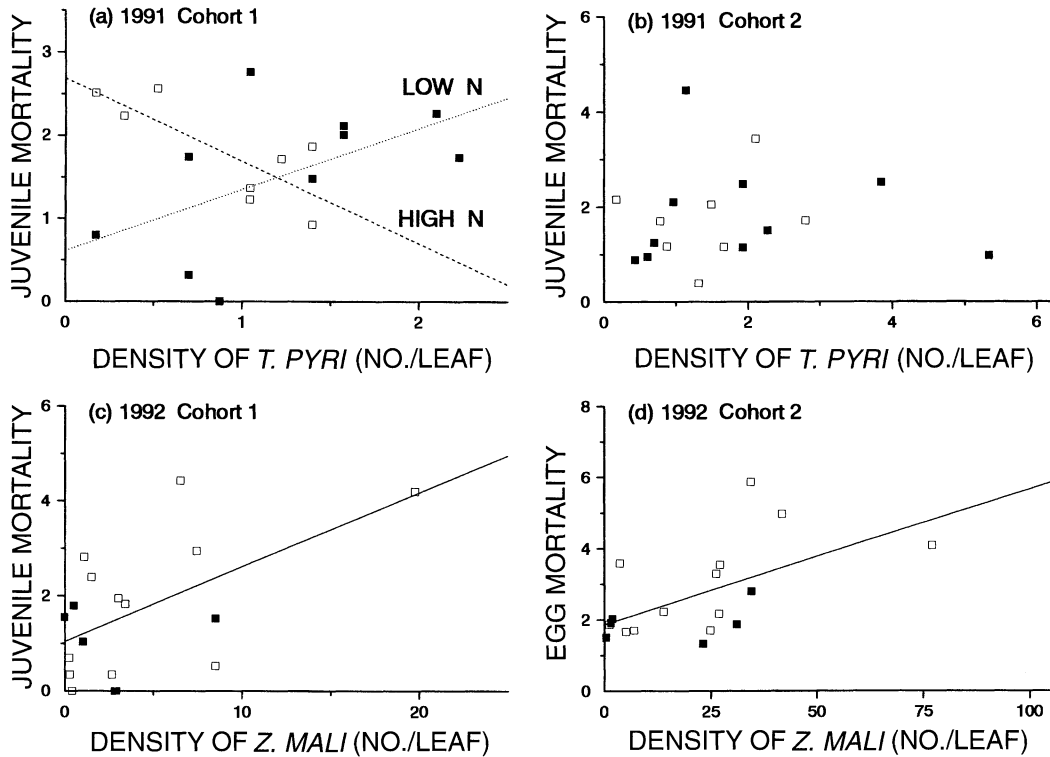


FIG. 3. Relationship between within-cohort mortality of *Panonychus ulmi* and cumulative density of predators. ■ low N (<2.4% of leaf dry mass); □ high N ($\geq 2.4\%$ of leaf dry mass). (a) Juvenile mortality depended on an interaction between N level and density of *Typhlodromus pyri* ($P = 0.021$) (1991: Cohort 1). (b) Juvenile mortality was not related to density of *T. pyri* ($P = 0.937$) (1991: Cohort 2). (c) Juvenile mortality increased with density of *Zetzellia mali* ($P = 0.019$) (1991: Cohort 1). (d) Egg mortality increased with density of *Z. mali* ($P = 0.013$) (1992: Cohort 2).

appeared that predators played little role in determining mortality of this stage.

Both predators were linked to observed abundance patterns in the second cohort of 1992. Abundance of *P. ulmi* eggs was negatively correlated with *Z. mali* density (Table 3). Egg mortality also increased with density of *Z. mali* ($P = 0.013$) (Fig. 3d), and there was some evidence for a negative interaction between *Z. mali* and *T. pyri* ($P = 0.108$). Juvenile and adult densities were negatively related to both *Z. mali* and *T. pyri*, and in addition there was a significant interaction between the predators (Table 3). Juvenile mortality was not significantly correlated with the density of either predator (*T. pyri*: $P = 0.352$; *Z. mali*: $P = 0.110$).

Juvenile mortality tended to be density dependent, particularly in 1992 (Fig. 4), while egg mortality was never density dependent. In 1991, there was only a very weak tendency for mortality of juveniles in the first cohort to increase with density, and there was no evidence for density dependence in the second cohort (Fig. 4a and b). In 1992, however, juvenile mortality was clearly density dependent for both cohorts (Fig. 4c and d).

Response of the predators to nutrient manipulation

The response of the predators *T. pyri* and *Z. mali* to changes in nutrient regime was evaluated in two ways. First, I looked for a direct response by testing for differences in cumulative density among fertilizer treatments and for a relationship between cumulative density and nitrogen concentration. Second, I looked for differences in the numerical response of the predators under the different fertilizer regimes by plotting predator versus prey abundance over the season (Fig. 6). Differences in response among treatments were evaluated statistically by comparing the ratios of predator to prey on each date.

Typhlodromus pyri.—Cumulative densities of the predator *T. pyri* did not vary significantly with fertilizer treatment in either year (Fig. 5, Table 2). The numerical response of *T. pyri* to changes in density of *P. ulmi* did differ under the different fertilizer regimes (Figs. 6a and b). As *T. pyri* does not consume *P. ulmi* eggs, abundance of *P. ulmi* was calculated using post-egg stages. In 1991, predator-prey ratios were significantly lower on the unfertilized trees in mid-July, but *T. pyri* increased in abundance on these trees relative to prey

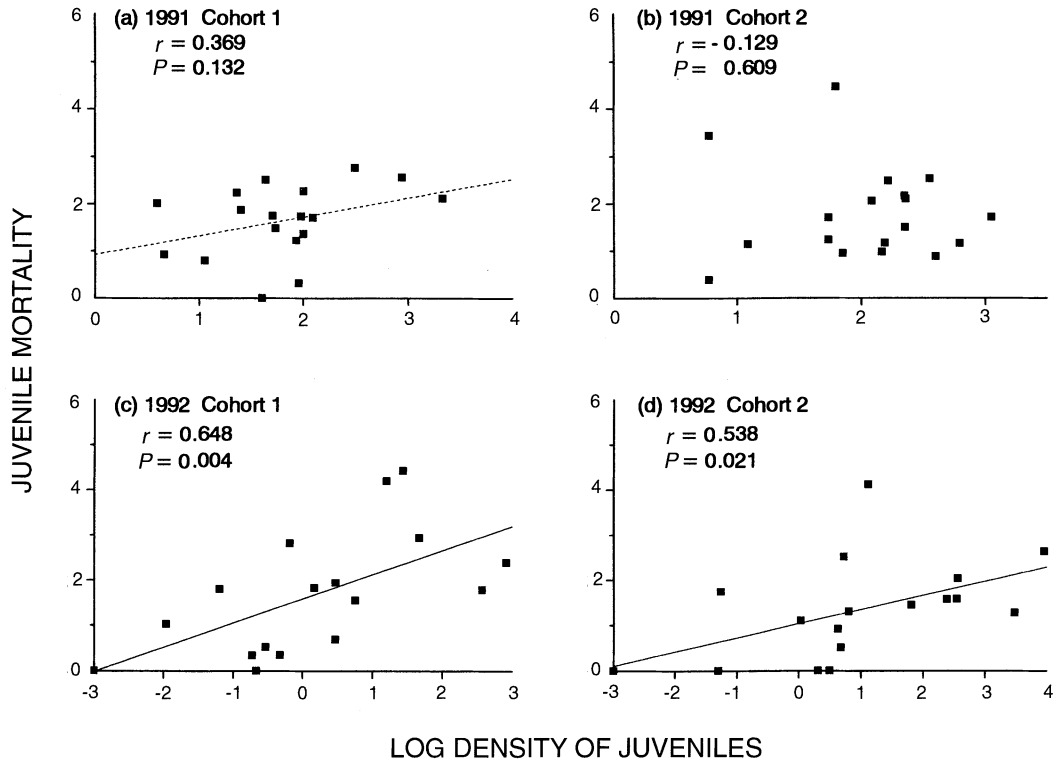


FIG. 4. Density dependence in juvenile mortality for *Panonychus ulmi*. Mortality (k -value = difference in log cumulative density) vs. log cumulative density (measured as number per leaf) for (a) 1991: Cohort 1, (b) 1991: Cohort 2, (c) 1992: Cohort 1, (d) 1992: Cohort 2.

density such that by early August, there were significantly more *T. pyri* per *P. ulmi* on the unfertilized trees (Fig. 6a). In 1992, there were again significantly more predators per prey late in the season (August–September) on the unfertilized trees (Fig. 6b). On unfertilized trees, *T. pyri* showed evidence of a delayed density-dependent response, while the pattern on fertilized trees was not consistent.

Zetzellia mali.—Cumulative densities of the predator *Z. mali* increased with nitrogen concentration in 1992 ($P = 0.023$) (Fig. 7). The effect of fertilizer regime on the numerical response of *Z. mali* to changes in density of *P. ulmi* was similar to that of *T. pyri* in 1992, with a stronger response on the unfertilized trees. The ratio of *Z. mali* to *P. ulmi* (eggs) was significantly higher on the unfertilized trees on sampling dates from 8 June through 31 August (Fig. 6c).

DISCUSSION

Previous work had suggested that while interpopulation processes could influence the dynamics of *P. ulmi* populations, within-population processes might be critical to explaining certain aspects of the dynamics, particularly the tendency for populations to go extinct (Walde 1991, 1994). In this study I tried to perturb within-population processes by altering the nutritional quality of the host plant. The primary objective, there-

fore, was to look at the response of the predator *T. pyri* to changes in density of *P. ulmi*, and at changes in predator impact, under conditions leading to different population growth rates of *P. ulmi*. Manipulations were conducted under field conditions that allowed for interactions, not only between the two species of primary interest, but also among other predators and competitors. A series of complex interspecific interactions emerged, and many of the relationships varied over time. Below, I first point out the most consistent patterns in the resulting interactions among nutrients, prey, and predators. I then discuss the implications of the results with respect to current understanding of predator–prey dynamics in this system.

The herbivore–plant interaction

Application of nitrogen fertilizer increased leaf nitrogen concentration, from 2.0% of dry mass in the unfertilized plots to 2.5% in the fertilized plots in 1991, and from 1.5% to 2.7% in 1992. The target N content for MacIntosh trees in this region is 1.9–2.2% in late July, so N can be considered adequate in 1991 and sub-optimal in 1992 in the unfertilized plots, and at luxury levels in the fertilized plots in both years.

Plant-eating arthropods are in general limited by the nitrogen content of their food plants rather than by phosphorus or by total biomass (Mattson 1980). Lab-

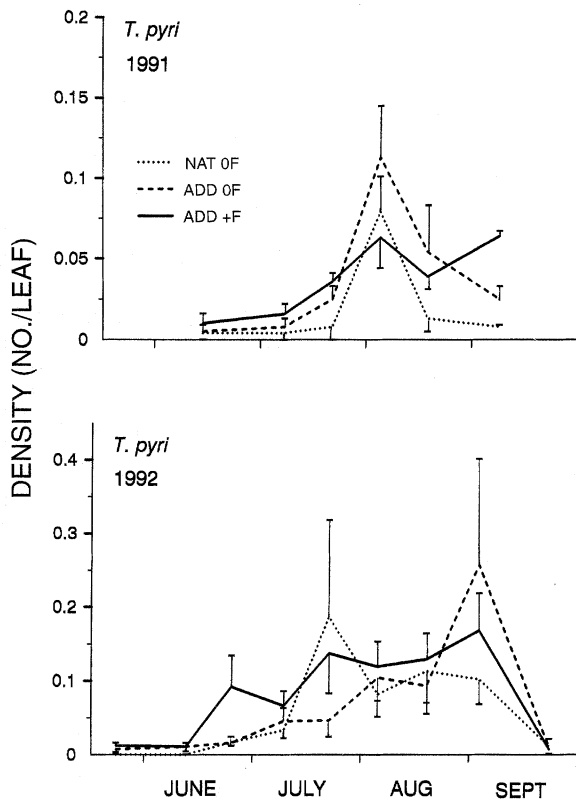


FIG. 5. Seasonal change in average density of the predator *Typhlodromus pyri* in 1991 and 1992. Experimental regimes were: (1) Natural density of *P. ulmi* (NAT), no fertilizer (OF), (2) *P. ulmi* augmented (ADD), no fertilizer, (3) *P. ulmi* augmented, fertilizer added (+F). Densities are means of the six plots for each of the treatments, and error bars are 1 SE.

oratory work with *P. ulmi* has established that the oviposition rate of *P. ulmi* increases with increased nitrogen content of apple leaves (Kuenen 1948, Breukel and Post 1959, van de Vrie and Boersma 1970). The results of the present study are consistent with this pattern, where the egg to female ratio tended to be higher on fertilized trees.

In the absence of intense competition or of interfering agents such as predators, an increase in egg production should translate into an increase in population density. In the second year of the study there was the expected positive relationship between leaf nitrogen and abundance of *P. ulmi*. The initial negative relationship between *P. ulmi* densities and level of nitrogen was not expected. One plausible explanation is that the response to nitrogen by *P. ulmi* is nonlinear, as has been shown for *Tetranychus urticae* to nitrogen (Rodriguez 1964) and to drought stress (English-Loeb 1989). In 1991, when either a negative or no relationship was seen between density and nitrogen, the nitrogen levels ranged more or less continuously from 1.8 to 2.7% of leaf dry mass. In 1992 a broader range was achieved, from 1.2 to 2.9%, but with a gap from 1.6 to 2.3%. Over the wider range of nitrogen concentra-

tions, density did tend to increase; however when only the upper range was considered, a negative relationship was seen in the second year as well. The two years are not quantitatively comparable and thus the data cannot be pooled to look for an overall nonlinear pattern, but it is at least plausible that over the lower range of nitrogen levels, the density of *P. ulmi* may increase with N, while at higher levels, density may actually decline. Earlier studies on the response of *P. ulmi* to nitrogen did not report a nonlinear relationship between nitrogen and either oviposition or survivorship, but these studies used either a restricted range of nitrogen concentrations (<2.5%), or used only two levels of nitrogen (Kuenen 1948, Breukel and Post 1959, van de Vrie and Boersma 1970). Two studies present results that are somewhat suggestive of a nonlinear response; Rodriguez's data (1958) suggest that densities either leveled off or declined above 2.6–2.7% N, and when Putman (1964) compared levels of 2.4% and 3.6% N in peach leaves, he found no effect on oviposition or mortality. Thus a nonlinear response appears to be a likely, although far from proven, explanation for the negative relationships seen in the first year of this study.

The predator–prey–nutrient interaction

Changes in nutrient content of the leaves did not directly affect the density of the predator *T. pyri*, but *Z. mali* densities were positively correlated with nitrogen in 1992. There were also significant impacts of nutrients on the predator–prey interactions. Both predators tended to have a greater impact on *P. ulmi* populations under low N. Mortality could be linked to *T. pyri* densities in 1991 only when N concentrations were low, and the correlation between density of juvenile *P. ulmi* and density of *Z. mali* in 1992 was most negative at low N. In addition, both predators showed a stronger numerical response, i.e., attained higher numbers relative to their prey when N levels were low. For the purposes of this study I defined numerical response simply as an increase in predator–prey ratio regardless of the mechanism that might have led to higher relative predator abundances. The mechanisms leading to the numerical response shown by *T. pyri* have been studied in the laboratory. Oviposition rate of *T. pyri* increases markedly with prey consumption (Hayes 1988), but except at extremely low *P. ulmi* densities, development rate and mortality of the predator are little affected by prey consumption (Hayes and McArdle 1987, Hardman and Rogers 1991). In this study I wanted to determine to what extent a numerical response by *T. pyri* is seen under field conditions, when the change in number of *T. pyri* may be influenced by more factors than just changes in the density of *P. ulmi*. Thus the lower number of predators relative to prey in the fertilized treatment suggests that under conditions leading to higher prey population growth rate, predators did not keep up as well with increases in prey density. Thus while *P.*

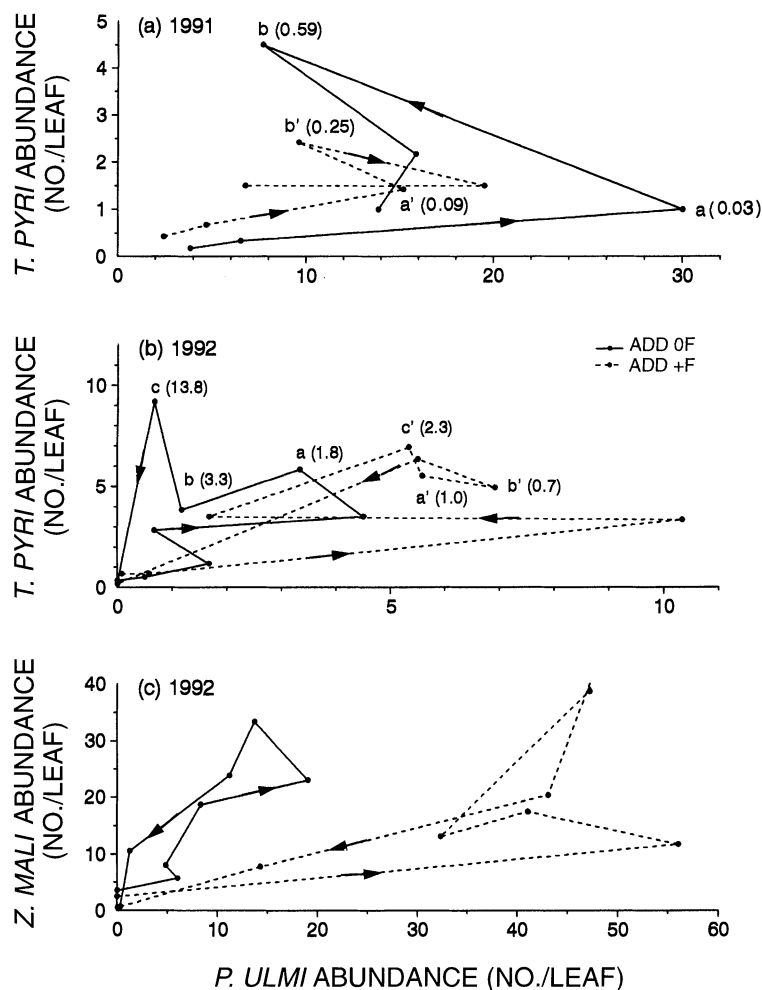


FIG. 6. Seasonal change in relative prey and predator abundances. (a and b) Abundance of the predator *Typhlodromus pyri* vs. abundance of post-egg stages of *Panonychus ulmi* in 1991 and 1992. Dates on which predator-prey ratios were significantly different ($P < 0.05$) between treatments are denoted as a, a', etc, with the ratio in parentheses. (c) Abundance of *Zetzellia mali* vs. abundance of *P. ulmi* eggs in 1992. On all dates except the first and last predator-prey ratios were significantly higher in the unfertilized treatment.

ulmi was kept well below economically important levels in all treatments (750 cumulative mite-days per cohort), and much below levels typically seen in orchards without these predators, densities became higher under high nitrogen conditions, indicating that neither *T. pyri* nor *Z. mali* compensated fully for the increased population growth rate of *P. ulmi*.

The prominence of the secondary predator *Z. mali* in determining the density and mortality of *P. ulmi* was unexpected. In 1992 densities of all stages (eggs, juveniles, and adults) were negatively related to densities of *Z. mali*. In addition, juvenile mortality of *P. ulmi* in the first cohort was positively correlated with density of *Z. mali*, and was density dependent. These strong effects were somewhat surprising as *Z. mali* is not usually thought to be an effective predator of *P. ulmi* due to low mobility and low rate of increase (Santos and Laing 1985). Recent experimental results from Oregon,

however, also suggest that the importance of *Z. mali* may have been underestimated (Croft and MacRae 1992, 1993). Prey densities were very low in the second year of this study, and *Z. mali* may be particularly effective at low prey abundances. Significant interactions between *T. pyri* and *Z. mali* indicate that the predators may interfere with each other, a pattern also observed by Croft and MacRae (1992, 1993).

Predator-prey dynamics

Finally, what can be concluded about the predator-prey dynamics of this biological control system? First, is it necessary to include consideration of plant nutrition when attempting to explain biological control of *P. ulmi* in apple orchards? The answer appears to be a qualified Yes for a quantitative explanation. Both nutrient levels and predator densities contributed significantly to explaining densities of *P. ulmi* over the

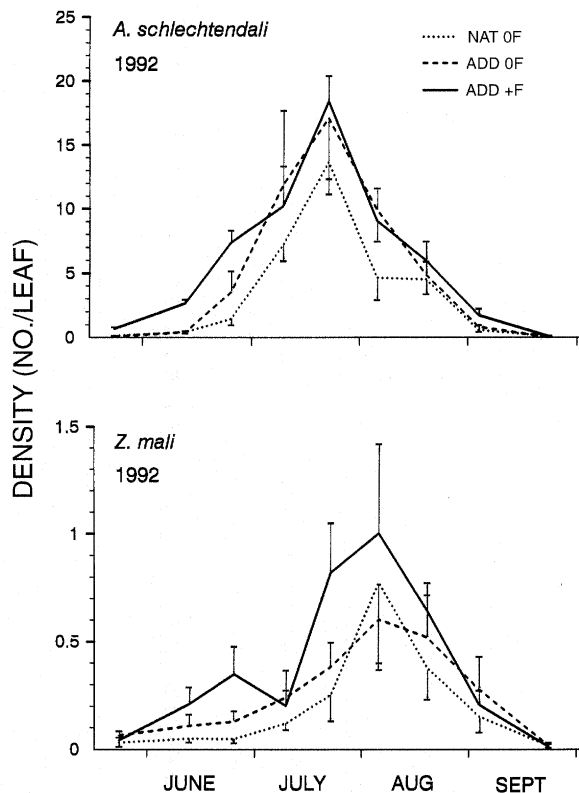


FIG. 7. Seasonal change in average density of *Aculus schlechtendali* and *Zetzellia mali* in 1992. Experimental regimes were: 1) Natural density of *P. ulmi* (NAT), no fertilizer (OF), 2) *P. ulmi* augmented (ADD), no fertilizer, 3) *P. ulmi* augmented, fertilizer added (+F). Densities are means of the six plots for each of the treatments and error bars are 1 SE.

course of the experiment, and the impact of the predators sometimes varied with the nutrient regime. However, successful biological control was clearly achieved irrespective of nutrient regime in both years.

Second, does altering the growth rate of the prey population affect the overall dynamics of the predator-prey interaction? Previous experiments suggested that without immigration *P. ulmi* populations tend to be driven extinct at the spatial scale of small trees, and perhaps also at the scale of mature trees (Walde 1991, 1994, Walde et al. 1992). Due to the distance between trees, their small size, and the low density of the prey populations, migration among trees should have been minimal in this experiment (Walde 1991, 1994), and thus the dynamic patterns can be attributed to processes occurring within populations, i.e., at the spatial scale of individual trees. Was stability affected by experimental changes in within-population processes? The magnitude of the numerical response of the predators was reduced under high nitrogen and this led to higher densities of *P. ulmi*. However, persistence of these *P. ulmi* populations was not significantly affected; that is, although the response of the predators was somewhat slower under high nitrogen levels, prey were driven to

very low levels relatively early in the season regardless of nutrient regime. (In orchards without predators, populations of *P. ulmi* are typically still increasing in abundance in mid-August.) Thus changes in population growth rate did not significantly affect at least one aspect of the fundamental dynamics of the predator-prey interaction, the probability of persistence.

On the other hand, there was evidence for spatial density dependence in mortality of juvenile *P. ulmi*. This potential source of stability was especially evident in the second year, when mortality was best correlated with *Z. mali* densities. Density-dependent mortality likely contributed to the smaller differences in density among treatments for later life stages of *P. ulmi* as compared with the egg stage in 1992. The importance of this density dependence to the overall dynamics of the system is not yet known, nor is it certain that *Z. mali* was the causal factor. However, it suggests that sources of stability may arise from within-population processes, as well as from migration. Evidence to date indicates that at the spatial scale of small trees, populations of *P. ulmi* tend to go extinct, which suggests that the density dependence is not sufficient to ensure persistence, although this is far from conclusively established. The importance of the secondary predator *Z. mali*, which appeared to play as prominent a role as *T. pyri* in 1992, was unexpected. *Z. mali* is at least as general in its feeding habits as is *T. pyri*. Local extinction of *P. ulmi*, when it occurs, is probably driven by the fact that its predators are generalist feeders, and the effect of a *Z. mali*-*T. pyri* complex may not be very different from that of *T. pyri* alone.

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