Distribution, Abundance, and Interspecific Associations of Typhlodromips sessor (Acarina: Phytoseiidae)

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ABSTRACT

Typhlodromips sessor DeLeon is the dominant phytoseiid in immature and unstable habitats throughout secondary succession in the Piedmont area of New Jersey. In fields approximately 1, 3, 5, and 10 years old, this mite had an average relative abundance of 95.4, 95.3, 82.8, and 72.3%, respectively. This ecological dominance was maintained in a 5-year-old field from June to October as population levels of this mite were consistently high and stable in comparison to the 13 other phytoseiid species collected there.

Analysis of the 175 plant species collected in these studies showed that T. sessor occurred in significantly greater densities upon herbaceous plants with thorny or

pubescent leaves. As a general predator, T. sessor was interspecifically associated with tetranychid mites, eriophyid mites, and Thrips tabaci Lindeman. A negative association was evident between this phytoseiid and predatory phloeothripid nymphs.

Geographically, T. sessor ranges from eastern Canada to Georgia and, according to Zack (1969), west to Missouri. Collection of 4584 adult phytoseiids along a transect of the east coast yielded 27 species, in which the average relative abundance of T. sessor was 89.8% in northern states, 50.7% in central states, and 0.8% in southern states.

Biological studies of Typhlodromips sessor DeLeon (Sciarappa and Swift 1977) show this phytoseiid to be a general feeder, preferring Tetranychus urticae Koch, Aculus schlechtendali (Nalepa), and Thrips tabaci Lindeman as prey for reproduction. Development time is relatively long, ovipositional rates low, and the species shows an adaptation to parthenogenecity. Continuing that study, one of the major objectives of the research presented here was to examine the distribution and abundance of this phytoseiid.

The current distribution and abundance of any animal is the result of interaction between 2 sets of factors—the past history of distribution and the bioecological requirements of the species (MacFayden 1963). Muma (1968) has dealt with the former factor in attributing distinct population differences among and discontinuous distributions within various litter communities to geologic or geographic differences. The latter factor is being studied in unpublished work from this laboratory, where distributions of many phytoseiid species are being related to successional stages, microhabitats, host plants, and physical parameters of the environment. Also, we suspect that differences in phytoseiid diversity may be related to community stability, since our unpublished data show that species richness and equitability of phytoseiids increase as the system progresses through secondary succession. Such an analysis of the Phytoseiidae, studied from the viewpoint of ecological succession and community stability, may contribute to our understanding of the attributes of effective biological control agents. We present here the results of a successional, seasonal, and geographical study relating to the distribution, abundance, and interspecific associations of T. sessor, the most abundant species in our area.

MATERIALS AND METHODS

Successional Study.—In the successional study, we chose natural sites in various stages of secondary development throughout the Piedmont area of New Jersey. These stages were newly-abandoned fields, young fields, mid-age fields, old fields, young forests, and climax forests. Newly-abandoned fields were in the 1st vr of secondary succession and were characterized by the dominance of annual herbaceous plants. Young fields were 2-3 yr into secondary succession and were distinguished on the basis of invasion by perennial herbaceous plants. Mid-age fields were ca. 4-9 yr old; dominants here were mainly perennial herbaceous plants such as goldenrods and asters. The old fields had been abandoned ca. 10 yr and were characterized by the invasion of woody plants such as red cedar, wild rose, dogwood, and sumac. We determined the successional stage of forest habitats by the dominance of various shrub or tree species common to the area's woodlands.

We sampled these various sites by selectively collecting those plants within the delineated area which appeared to be of frequent occurrence or appeared to contribute a large portion of the total biomass. These plants were clipped near the base of their stem or twig, identified to the species level, placed in large plastic bags according to plant species, and transported to the laboratory for extraction of the microarthropods. For this extraction, we used Berlese-Tungren funnels with 75-watt, variable intensity spotlights for drying the vegetation.

Seasonal Study.-For study of seasonal dynamics, we chose a 5-yr-old field on the periphery of Hutcheson Memorial Forest, East Millstone, N. J. We

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Table 1.—Relative abundance of T. sessor through secondary succession of the Piedmont in New Jersey.

			% relative abundance of <i>T. sessor</i>		
Successional stage	No. sites	No. phytoseiids	Mean	Range	
New field Young field Mid-age field Old field Young forest	3 3 5 3 3	108 467 1202 1015 698	95.4 95.3 82.8 72.3 8.0	91.396.0 93.795.8 73.794.7 64.975.9 0.010.8	

divided a center section of this field into six 10×15-m plots, then divided each plot into 6 subplots. One subplot per plot was collected from on each sample date. Sample dates were spaced at intervals of ca. 17 days during the period June 19-Sept. 17. On Oct. 5 and 25, we made general samples of the remaining green vegetation. Collection involved the use of a 1×1/4-m quadrat which we randomly placed 6 times in each designated subplot. We clipped all plants within the quadrat at the base of the stem and separated them to species. Each species was placed separately in its own plastic bag and transported back to the laboratory for individual extraction of the micro-arthropods. Since a non-selective extraction was desired in this study, we utilized a washing method. With this method, the foliage was immersed in a pyrethrum and spreader solution for ca. 18 h. Seven ml of the pesticide, Pyrenone Cropspray® (FMC Corporation, Middleport, N.Y.) containing 6% pyrethrins, and 3.5 ml of the spreader, Triton B-1956® (Rohm and Haas, Philadelphia, Pa.) were added to every 14,000 ml of water. This solution effectively penetrated very pubescent samples and stimulated the arthropods into activity, which facilitated removing them with copious sprays of water. The specimens were filtered out by passing the solution through a graded series of standard sieves and subsequently transferred to vials of 70% alcohol. After this extraction, we dried each plant sample separately to obtain dry weight data to be used in determining total plant biomass and animal density through time. Finally, we calculated coefficients of association between T. sessor and various micro-arthropods on the basis of presence or absence of a density level of 0.10 micro-arthropod per g plant. Since we used contingency tables that required an expected value of 5/cell, this arbitrary lower limit was necessary to maintain the validity of the chisquare test that followed (Cole 1949).

Geographical Study.—For the geographical range and abundance study, we sampled young fields of similar composition along a north-south transect at ca. 100-mi. increments throughout the eastern coastal states from Maine to Fla. We collected our samples by selecting those plants which provided favorable micro-habitats for phytoseiids, such as thistles, goldenrods, and asters. We extracted these plants in a portable, modified version of the washing ap-

paratus described previously. All samples in this study were taken in Aug. and Sept., both in our departing and returning trip along the transect route.

Microscopic Preparation.—For all the studies, we transferred the extracted material from storage vials to petri dishes for subsequent mounting in a modified Berlese mounting fluid (Schuster and Pritchard 1963). After heating and clearing, we examined the slides under a phase contrast microscope and identified the specimens to the species level for phytoseiids and to the family level or lower for the remaining animals.

RESULTS AND DISCUSSION

Successional Study .- In this study, we collected 3490 phytoseiids from 17 sites. The relative abundance of T. sessor, expressed in Table 1 as a percentage of the total phytoseiids in the sample, is initially high and then diminishes rapidly as the young forest stage is approached. This species rarely inhabits older forests. The ability of T. sessor to maintain a high relative abundance throughout the relatively rapid changes in plant and animal composition associated with secondary succession to an old field, shows the mite to possess superior adaptation to early successional communities. This ecological dominance is quite evident, since we collected 15 other phytoseiids in these same habitats but at generally lower relative abundances. Boughley (1973) points out that communities characterized by monoculture or those of recent origin tend to have few dominants. In this instance, the phytoseiid trophic levels within these field communities have been adapted to primarily by T. sessor; the other phytoseiids failed to establish sizable populations. We discuss biological reasons for this constancy and dominance in the section concerning interspecific associations, in a previous paper concerning feeding habits (Sciarappa and Swift 1977), and in a paper in preparation.

Geographical Study. — We examined 4584 adult phytoseiids from 51 early successional sites and found T. sessor in every coastal state from Maine to Ga. We established 3 distinct groupings of avg relative abundance covering the 27 phytoseiid species collected throughout this range. In the more northern states of Maine, N. H., Mass., Conn., N. J., and Del., populations of T. sessor averaged 89.8% relative abundance per sample. In the more central states of Md., Va., N. C., and S. C., a moderate decline to an avg relative abundance of 50.7% occurred. In the more southern states of Ga. and Fla., 8 samples were taken in which only one sample from northern Ga. contained T. sessor, for an avg relative abundance of 0.8%.

From Maine to S.C., the biomes, in order of descending latitude, are the coniferous-deciduous forest ecotone, deciduous forest, and oak-pine subclimax. Although the character of the early successional stages of these biomes varies from one to another, collectively they differ greatly when com-

pared to the pine sub-climax through Ga., and Fla. (Pitelka 1941). The differences between these 2 groups were reflected in the plant species collected, which gave rise to a new complex of phytoseiids dominated by Typhlodromalus peregrinus (Muma) and Phytoseius macropilus (Banks). From Del. southward, T. peregrinus becomes increasingly dominant and may be the ecological equivalent of T. sessor. In no area was a male of T. sessor collected. Thus, this mite's adaptation to parthenogenicity is of more than just local occurrence.

We determined geographical range, outside of this transect, by collecting samples in various areas. We extracted *T. sessor* from samples collected in Middleport, N. Y.; State College, Pa.; various parts of Ind.; and Guelph, Ontario, Canada. In the literature, *T. sessor* is reported as occurring as far west as Mo. (Zack 1969) and occurs in Tenn. and Ohio (DeLeon 1962).

Seasonal Study.—In this study, we collected a total of 3479 adults of T. sessor. Absolute density of this mite in each sample ranged from 39.3-103.0 adults/m2 of vegetation. The density of T. sessor was greater in the 2nd sample than in the last; otherwise, no significant (P = .01) differences were found. A declining density trend was obvious over the last 6 samples. Throughout the study, values of 1.82 to 3.00 were maintained in the adult to immature ratio. These slight changes in age-structure and density reflect a slowly fluctuating and highly stable population in this 5-yr-old field. In this system, the tetranychid populations showed no evidence of causing plant damage and populations ranged from 9.7-66.2 individuals per m2 throughout the season. Both Thrips tabaci and syrphid larvae were numerous in all samples ranging from 53.9-510.2 and 23.8-154.0 individuals per m2, respectively. Populations of tarsonemid mites fluctuated erratically. Phloeothripids

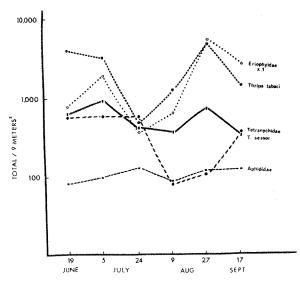


Fig. 1.—Population curves of important micro-arthopods in the 5-yr-old field used in the seasonal study.

Table 2.—Plant factors influencing distribution and abundance of *T. sessor* in a 5-yr-old field on the Piedmont of New Jersey.

Plant species	% composition	Density of T. sessor
Solanum carolinense	.7	1.315 a
Solidago rugosa	14.6	.795 b
Cirsium arvense	1.1	.703 bc
Plantago lanceolata	1.5	.670 bc
Achillea millefolium	1.3	.635 bcde
Potentilla recta	1.7	.465 cdef
Fragaria virginiana	4.9	.415 def
Aster simplex	8.4	.400 ef
Solidago canadensis	8.5	.400 ef
Solidago graminifolia	21.5	.368 fg
Andropogon species	1.3	.342 fg
Convolvulus arvensis	4.3	.328 fg
Aster ericoides	8.1	.293 fg
Penstemon species	1.3	.282 fg
Linaria vulgaris	1.6	.265 fg
Solidago juncea	11.9	.247 fg
Erigeron strigosus	1.4	.245 fg
Solidago nemoralis	2.3	.140 g
Hieracium florentinum	1.4	.133 g
Chrysanthemum leucanther	num 1.2	.125 g

^a Density calculated as mites per g plant dry weight transformed to log base 10. Means followed by the same letter do not differ significantly at P>0.05.

(probably Haplothrips subtilissimus) populations declined steadily. Two large bursts in spore production were noted. Total populations of T. sessor most closely paralleled its 2 primary prey, T. tabaci and eriophyids (Fig. 1). The population curves suggest that as these prey became less abundant, after providing resources for the highest predator populations, the predator then concentrated upon tetranychid prey which, in turn, proceeded to decline. We can say little about the remaining profusion of mites, insects, nematodes, crustaceans, and snails that were collected in erratic numbers and frequencies.

T. sessor.—Plant Associations.—In each study, data were obtained on the density of T. sessor on individual plant species to learn whether general relationships existed among plant species, or plant characteristics such as leaf structure, and population of T. sessor. In the successional study, we sampled 169 plant species in the various habitats. The avg densities of T. sessor extracted from these 82 herbaceous species and 87 tree and shrub species were 17.41 and 4.59 individuals per standard volume, respectively. In the seasonal study, we consistently collected 20 herbaceous species and a number of infrequently-occurring species. The growth of these plants over the season led to progressively larger sample biomasses, but this was not correlated with population growth of T. sessor. However, these populations seemed to be correlated with plant leaf characteristics (Table 2). The 1st 7 plants had greatest mite densities and were characterized by having leaves much more thorny, hairy, or pubescent than the remaining 13 species. This association at the microhabitat level may be attributable to more favorable humidities at the leaf surface or possibly easier access to feeding upon plant juices. Indirect relationships may involve increased prey populations or increased protection from natural enemies.

This preference for certain plant species provides a distinct parameter for determining the abundance and distribution of T. sessor, which is further modified by the distribution of the plants themselves. For example, the most important plant in this field with respect to T. sessor was Solidage rugosa (Table 2). This species contributed 14.6% of the total plant biomass but harbored 26.8% of the total population of this phytoseiid. On the other hand, S. graminifolia composed the highest percentage biomass (21.5%) but, due to lower mite densities, harbored only 16.5% of their total populations. Thus, with all other factors held constant, the T. sessor population levels of any field may be a direct function of its plant composition.

T. sessor.-Micro-arthropod Associations.-In the seasonal study, populations of T. sessor were highly and positively associated with 3 common phytophagous species-tetranychid mites, eriophyid mites, and Thrips tabaci. The coefficients of interspecific associations, and corresponding chi-square values in parentheses, for these micro-arthropods were: tetranychids-0.525 (0.975); eriophyids-0.388 (0.95); and Thrips tabaci-0.404 (0.99). We have shown these 3 micro-arthropods to be highly preferred sources of prey in terms of reproduction (Sciarappa and Swift 1977), and there appears to be correlations in the population, as shown in Fig. 1. Therefore, it is likely that these associations represent predator-prey interactions in which the predator cannot rapidly eliminate the prey, but maintains a casual relationship that conserves prey populations. Tetranychids and eriophyids were generally present in low densities, but were present in high frequencies of 77.5 and 66.7%, respectively. T. tabaci had the highest frequency of 82.4% but, more importantly, had a total biomass much larger than any other microarthropod. We note the contrast between the fluctuation in the 3 preferred prey populations and the consistency of the T. sessor population (Fig. 1). Be-

sides other biological and environmental limitations, high populations of these prey may have been limited by the consistently high predator populations acting in a regulatory manner. It has been contended by Elton (1929) and others that predators feed most heavily upon the most abundant prey. As some prey populations become more abundant, they also become more subject to predations which may limit their increase. Murdoch (1969) has examined possible mechanisms whereby predators switch the greater proportion of their attacks to another prey which has become the most abundant. This process may further limit a rapidly increasing prey population and tend to limit the reduction of the initial prey species. Such factors may be operating within this community and will be investigated more fully in a forthcoming paper.

We found a coefficient of interspecific association of 0.502 at a chi-square value of 0.95 for populations of *T. sessor* and macrochelid mites. This association might represent a similarity of adaptation and environmental response. Macrochelids are general predators; however, their niche is focused primarily upon predation in the soil and litter (Krantz 1971, Wallwork 1970). Populations of *T. sessor* were not statistically associated with tarsonemid mites, aphids, syrphid larvae, or anthocorids (*Orius* species), although subtle and important relationships may exist.

Populations of T. sessor were negatively associated with populations of phloethripid nymphs (note: only adult thrips could be identified to species). These thrips, identified by Dr. Sueo Nakahara as Haplothrips subtilissimus Haliday, are known predators of mites. The coefficient of -.318 was weakly significant at P=0.25. This association represents interspecific competition of the direct interference type. Each predator consumes similar prey, as well as one another (Sciarappa and Swift 1977). This functional niche overlap may have led to a distinct spatial separation in niche.

Other phytoseiid species were relatively scarce in this seasonal study, as seen in Table 3 of relative abundances. T. sessor generally averaged over 90%

Table 3.—Relative abundances of phytoseiid mites through time in a 5-yr-old field on the Piedmont of New Jersey.

	June 19	July 5	July 24	Aug. 9	Aug. 27	Sept. 17	Oct. 5	Oct. 25
	95.0	98.3	96.6	81.0	92.8	79.5	75.4	64,3
Typhlodromips sessor	0.3	90.0	2.5	18.7	5.5	19.4	22.3	34.7
Galendromus pomi (Parrott)	3.3	0.1	2.5	0.2			*********	********
Proprioseiopsis sarraceniae (Muma)	3.3	1		0.2	0.2		2.3	
Phytoseius macropilis (Banks)		.1			2			0.9
Typhlodromalus peregrinus (Muma)	.6 .3	.8	0.5					
Proprioseiopsis mexicanus (Garman)	.S	.0	0.5		.9	********		
Proprioseiopsis dorsatus (Muma)	, <u>1</u>	.1	5					
Veoseiulus fallacis (Garman)	.1					0.9		
Veoseiulus umbracticus (Chant)					3		******	
Amblydromella nodosus (DeLeon)		.3						
Proprioseiopsis clausae (Muma)		.2			*******			
Propriosciopsis SD.	1	.2				-		
Typhlodromina conspicua (Garman)	.1	*****				.2	-	.1
Veoseiulus sp.	-						4.47	277
Fotal no. collected	689	943	407	443	842	458	447	377

relative abundance, even though 13 other phytoseiid species invaded the field at one time or another. Only at the end of the season did one species, Galendromus pomi (Parrott), become established, possibly as a result of dispersal from nearby deciduous trees, where it probably fed upon tetranychid and eriophyid mites (Specht 1968). This species especially favored Solidago gigantea with its large number of eriophyids. G. pomi populations steadily increased their relative abundance from the end of July through Aug. and Sept., leading to a 34.7% composition in late Oct. Aside from the late surge in populations of G. pomi, no other phytoseiids became abundant during the study.

The ability of *T. sessor* to survive so successfully while other species fail to develop more than sporadic colonies establishes *T. sessor* as the superior competitor under these bio-ecological conditions. Specific adaptations of *T. sessor* towards survival in this early successional field include parthenogenecity, cannibalism, low reproductive rates, a generalist foraging strategy, and a casual but close association with prey. Overall, this biological profile reveals an organism well adapted to living in a changing, early successional habitat where density-dependent mechanisms and overall fitness may be uncommon, but still advantageous.

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