AN ABSTRACT OF THE THESIS OF

Willard B. Strong for the degree of Doctor of Philosophy in Entomology presented on April 27, 1995. Title: Biological Control of *Tetranychus urticae* Koch in Hops by Phytoseiid Mites: Feasibility, Spatial Aspects of Interactions, and Management.

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Brian A. Croft

Densities and damage by *Tetranychus urticae* Koch (TSSM) and levels of phytoseiid mites on hops, a rapidly growing perennial plant, were assessed in 34 commercial fields and 11-19 sites of escaped hops in the Willamette Valley of western Oregon in 1991-1992. TSSM were present at low densities in most escaped hop sites, but reached high densities in commercial fields. On escaped hops, the most common phytoseiid was *Typhlodromus pyri* Scheuten, which was probably a vagrant from surrounding vegetation. *Neoseiulus fallacis* (Garman) was most abundant in commercial hops, making up 88% of all specimens. *Amblyseius andersoni* Chant and *Galendromus occidentalis* (Nesbitt) were the other common phytoseiids found. Phytoseiids appeared to be suitable biological control agents for commercial hop use.

In 1992-3, inoculative introductions of these phytoseiid species, singly or mixed, were made into individual hop plants. The most effective TSSM control was by *N. fallacis* or *G. occidentalis* or a mixture of both species, although *G. occidentalis* was less beneficial in 1993. *T. pyri* and *A. andersoni* provided some control, but always less than *N. fallacis* and *G. occidentalis*. Both *N. fallacis* and *G. occidentalis* dispersed throughout hop plants if TSSM were scarce, but they stayed on the lower parts of the plant when TSSM were abundant.

In 1993-4, the timing of introductions of *N. fallacis*, the height of release on the plant, overwinter survival and some cultural factors were investigated to determine the optimal use patterns for this predator. Release height seemed to be unimportant, but release timing was influential in conditions of unusually low or high TSSM densities. *N. fallacis* overwinters in hop fields, but early spring cultural practices inhibit survival to summer. Other cultural practices were detrimental to biological control during summer. Predators released into 0.5 ha plots in commercial fields

reduced TSSM to commercially acceptable levels. The predator-prey interaction is defined by local extinction/recolonization phenomena, potentially lending within-season persistence to biological control.

Biological Control of *Tetranychus urticae* Koch in Hops by Phytoseiid Mites: Feasibility, Spatial Aspects of Interactions, and Management.

by

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Major Professor, representing Entomology

Redacted for Privacy

Chair of Department of Entomology

Redacted for Privacy

Dean of Graduate School

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BIOLOGICAL CONTROL OF *TETRANYCHUS URTICAE* KOCH IN HOPS BY PHYTOSEIID MITES: FEASIBILITY, SPATIAL ASPECTS OF INTERACTIONS, AND MANAGEMENT

1. INTRODUCTION

The two-spotted spider mite (TSSM), *Tetranychus urticae* Koch, is one of the main pests in hop culture worldwide (Neve 1991). It feeds on the foliage, resulting in chlorosis and reduced photosynthesis (Helle & Sabelis 1985). Infestations can reduce the yields and quality of cones, the harvested portion of the crop.

Control of TSSM outbreaks has historically relied on applications of broad-spectrum acaricides (Campbell et al. 1987). These applications often reduce the populations of predacious mites in the family Phytoseiidae (Campbell 1985, Cranham 1985). In addition, broad-spectrum insecticides directed against the hop aphid, *Phorodon humuli* (Schrank), which can decimate populations of macropredators (insects) that also play a role in TSSM regulation (Aveling 1981, Campbell 1985, Gesner & Zeleny 1984, Kalushkov & Zeleny 1986, Zeleny et al. 1988). As a result, TSSM populations in hop fields are highly unstable and subject to secondary or induced outbreaks. Furthermore, TSSM have become resistant to many acaricides formerly used against it (Borovoi 1981, Cranham 1974, Croft 1990, Muir & Cranham 1981), restricting the available control measures.

Recently, the development of more selective pesticides has allowed the establishment of natural enemy populations in hop fields (Campbell 1988). Research into the use of these natural enemies has been largely confined to surveys of their incidence in commercial hop fields (e.g. Ruzicka et al. 1986, Ruzicka et al. 1988, Zeleny 1978). The predominant biological control agents for aphids were from the insect families Coccinellidae, Anthocoridae, and Aphidiidae. Although these species were sometimes found in high densities, the general conclusion was that they were unable to maintain aphids at low densities. Campbell (1990) unsuccessfully attempted to release coccinellids and chrysopids against hop aphid.

Naturally-occurring biological control agents against TSSM were mostly from the insect and mite families Anthocoridae, *Stethorus* spp. (Coccinellidae), and

Phytoseiidae (Cranham 1985, Maier 1993, Zeleny 1981). The phytoseiid, *Typhlodromus pyri* (Scheuten) seemed to provide some regulation of TSSM, but the data were inconclusive (Maier 1993).

Several attempts have been made to release phytoseiids into commercial fields. In Washington State, Pruszinski and Cone (1972) released *P. persimilis* into hops, but concluded that it was ineffective, probably due to the low humidities encountered in that hop-growing region. They also found that the dominant naturally-occurring phytoseiid in Washington was *Galendromus (=Metaseiulus) occidentalis* (Nesbitt), but it did not regulate TSSM to low densities (Pruszinski & Cone 1973). Augmentative releases of *G. occidentalis* were not attempted.

Mori et al. (1990) found that *Typhlodromus longispinosus* Evans provided some suppression of TSSM in hops in Japan. In New Zealand, augmentative releases of *P. persimilis* were studied for several years; the phytoseiids maintained TSSM to low levels in at least one year, and release recommendations are currently made to hop growers (Beatson 1992). In Germany, *P. persimilis* was released into hops and provided some suppression of TSSM, but not enough to be commercially viable (Kremheller 1991). Campbell (1990) released *P. persimilis* into hops in England. They were unsuccessful at maintaining TSSM in normal hop plants, but showed promise in "dwarf" plantings (2.25 m tall instead of the normal 6 m), possibly due to the higher humidities encountered in these plantings.

Despite these generally poor results and the negative attitude towards the potential for biological control of TSSM on hops (Cranham 1985), I felt that the problem may have been with the natural enemy selected (usually *P. persimilis*). There are some theoretical considerations in selecting a natural enemy for use against TSSM in hops. In any biological control system, success is dependent upon host (prey) acceptability, host association, climatic compatibility, seasonal coincidence, and other factors (van den Bosch et al. 1982). Many studies have demonstrated the suitability of Tetranychidae as prey for phytoseiids (Helle & Sabelis 1985). Phytoseiids are multivoltine, and have diapause characteristics similar to many tetranychids (Overmeer 1985), so seasonal coincidence is not inhibitory. Many species of phytoseiids are negatively influenced by low humidities (Croft et al., 1993), which has been posited as a reason for the lack of success of phytoseiids in hops in the past (Campbell 1990). Furthermore, spatial association of phytoseiids with TSSM on hops may be poor. Hops grow rapidly from ground level in spring to a height of 6 m by July. Both predators and prey must disperse up this rapidly expanding plant. Spider

mites readily disperse to the tops of plants and reach high populations there (Burdajewics & Cone 1972, Sites & Cone 1985), while *G. occidentalis* remain closer to the bottoms of the plants. The restricted vertical dispersal of phytoseiids has also been noted by Campbell (1990), Mori (1990), and Blackmer (1994). In order to use phytoseiids against TSSM, then, a species would need to be found and managed in a way to overcome the humidity and spatial coincidence problems observed in hops.

The persistence of the predator-prey interaction is another consideration in developing a biological control program. Phytoseiid-tetranychid interactions are known to be unstable on small spatial scales (Sabelis & Laane 1986, Dieknam et al. 1988), with phytoseiids overexploiting the prey, the prey declining to extinction, then the phytoseiids starving to extinction (Sabelis & van der Meer 1986). If this were to occur across a field, pest suppression would be cursory at best. However, there is a growing body of evidence suggesting that several characteristics can result in persistence over large scales of locally unstable interactions (DeAngelis & Waterhouse 1987, Jansen & Sabelis 1992). These characteristics include predator and prey dispersal, local extinction and recolonization, asynchrony of the local populations, and the incidence of empty habitat patches (Taylor 1988). The existence of these metapopulation characteristics would indicate that persistence over large spatial scales (e.g. a field) is possible.

The goals of this research were to identify suitable species of phytoseiid for biological control of TSSM in the Willamette Valley of Oregon, USA; to determine their potential for regulating TSSM to low levels; to test factors associated with phytoseiid introduction and crop culture which might be important in the success of biological control; to assess the intraplant spatial association of phytoseiids and TSSM; and to determine the potential for regional (field-wide) persistence of the predator-prey system. These goals were achieved in three research efforts. The first, conducted in 1991-2, was a survey of escaped (uncultivated) domestic hops and cultivated commercial hops for the incidence of TSSM and phytoseiids. In 1992-3, I tested the predominant phytoseiid species for effectiveness in maintaining TSSM at low levels in commercial fields. I also gathered data during this time to assess dispersal and the spatial relationships between the predator, TSSM and the hop plant. In 1993-4, I tested several variables associated with predator introductions and crop culture which might influence the outcome of biological control. I also made some larger-scale releases to assess the behavior of the system under these conditions; in

this experiment I also collected data to determine the potential for persistence of biological control over larger spatial scales.

2. PHYTOSEIID MITES ASSOCIATED WITH SPIDER MITES ON HOPS

INTRODUCTION

Two-spotted spider mite (*Tetranychus urticae* Koch) (TSSM) is a major pest of hops and associated crops in the Willamette valley, Oregon. It overwinters on dead plant materials or on the hop crown, emerging in early spring to feed on weeds and new hop shoots (Cone et al. 1986, Cranham 1985). Control of TSSM usually requires from one to several miticide sprays each summer. Other pesticides such as aphicides sprayed for hop aphid (*Phorodon humuli* (Shrank)) and fungicides used for disease control also may affect TSSM and its predators (Croft 1990). Because of pesticide resistance in TSSM (Campbell 1985), chemical control has been difficult. A biological control program for TSSM would be a desirable alternative to replace pesticides or to augment their use.

Several biological control agents against TSSM have been reported from hops in arid regions of western North America, but their usefulness has been limited because of non-selective pesticide use (Pruszynski & Cone 1972). These include insect predators and phytoseiid mites. In central Washington, *Galendromus occidentalis* (Nesbitt) was the most common phytoseiid found; it emerged from crowns in early April and then became sparse, reappearing in July (Pruszynski & Cone 1973). Although there appeared to be some pesticide tolerance in the central Washington strain of *G. occidentalis*, it did not maintain TSSM at low densities.

Little is known about biological control on hops in the mild, more humid hop-growing region in Oregon. This study was conducted to determine the beneficial species composition and the incidence of phytoseiids and spider mites on escaped and commercial hops in Oregon, to measure early spring mortality of phytoseiids, and to monitor dispersal of phytoseiid and TSSM within and between hops and other crops.

MATERIALS AND METHODS

Commercial Fields Survey

Thirty-four commercial hop fields were surveyed 3 times each in 1991 and again in 1992. From each field, 50 leaves were taken, 5 from each of 10 plants located near support poles. These poles support wires at a height of 6 m, from which heavy twine is suspended; hop vines grow up the twine. Cracks in these wooden poles and in debris at the soil-pole interface are overwintering sites for TSSM (Cone et al. 1986) and presumably for phytoseiids. Poles were selected from the field edge to about 50 m toward the field interior. In May, all leaves were collected from near the ground. In 1991, later samples were from 0-2 m, since TSSM (and phytoseiids) are concentrated in these areas at these times (Sites & Cone, 1985). Later samples were taken from the ground to 6 m.

Survey times were early-season (May 3-10 in 1991, May 18-28 in 1992), when basal leaves were present but before hop shoots started climbing the twine; mid-season (on June 14 in 1991, June 8-23 in 1992), when shoots had grown 2-3 m up the twine; and pre-harvest (Aug 3, 1991; Aug 17-18, 1992), when flowers formed on side-arms growing from the main hop stem.

All hop leaves were observed under a binocular microscope at 40X; all life stages of phytoseiids were counted and adults were mounted in Hoyer's solution (Krantz 1978) on a microscope slide for species identification. TSSM adult females were counted, and leaves were scored for damage on a scale of 0 to 5 (0= no damage, 1= light damage to one leaf lobe, 2= light damage to 2 lobes, 3= light damage to 3 or more lobes, 4= heavy damage to 3 or more lobes, and 5= heavy damage over entire leaf surface).

Escaped Hops Survey

Several sites in the Willamette Valley were found with escaped, unsprayed hops. Typical sites were in field headlands, road verges, and along ditches and fencerows. Most sites were near commercial hops or other crops, which could harbor spider mites or predatory mites. Hop leaf collections were made from 0-2 m; leaves with TSSM were selected where possible since these would be most likely to harbor phytoseiids. In the 1991 survey, 14 samples (from 11 sites) of 50 leaves each were taken between July 9 and August 5. In 1992, three surveys of 25 leaves per sample

were made on May 8 (13 samples), between June 8-18 (19 samples) and on July 29 (16 samples). All phytoseiids were counted and identified.

Early Spring Survival Study

A single field of the Perle variety of hops, which had large numbers of phytoseiids the previous fall, was selected. On March 16, before hop plants started growing (hop plants are perennial and die back to ground level every year), 4 pots of live bean plants in vermiculite were leaned against poles. Bean plants had light infestations of spider mites to attract phytoseiids. Plants were replaced with fresh plants on March 30, April 6 (2 extra pots were added to total 6), and April 13. On these dates hop leaves were also collected from new shoots. Hop leaves and bean plants were observed for mites, and phytoseiids were collected for identification.

Transect Surveys

Two commercial hop fields were selected to monitor dispersal of TSSM and phytoseiids from adjacent crops. One field (#27) had strawberry to the north (upwind); another field (#33) had strawberry to the northwest (upwind) and southeast (downwind) and blackberry to the northeast. At each hop/berry interface, 50 leaves were collected from a transect running from 40 m within the berry field to 40 m within the hop field. Five leaves were collected at each of 10 sites along the transect: at 0, 10, 20, 30, and 40 m from the interface. Leaves from hop fields were collected from plants near support poles. Predators were counted and each leaf scored for damage on the 0-5 scale described above. This procedure was repeated three times in 1991, on the same dates that commercial field surveys were taken.

RESULTS AND DISCUSSION

Commercial Fields Survey

TSSM were generally low in number in 1991, presumably due to the cool, wet weather that prevailed (Table 1). In early-season, 13 fields (38% of total) had infestations but mean densities of females per leaf in infested fields and mean damage ratings on infested leaves of infested fields were low. Only two predator specimens, both *N. fallacis*, were found in early-season. At mid-season, more fields had TSSM,

Table 1. *Tetranychus urticae* levels and phytoseiid mites found in commercial hop surveys, 1991-1992.

	1991			1992		
	Early	Mid	Late	Early	Mid	Late
Fields	34	34	34	32	31	29
% fields with mites	38%	76%	97%	81%	100%	86%
Mites/leaf in fields with mites[1]	.31±.16	.66±.25	3.15±.87	.91±.30	3.06±1.34	.93±.46
Mean damage on infested leaves in fields w/mites[1]	1.10±.13	1.30±.08	2.16±.27	1.29±.08	1.46±.08	1.70±.07
Phytoseiids/field[1]	.06±.04	.15±.09	2.85±1.87	.63±.37	3.65±1.57	25.2±14.5
A. fallacis	2		76	10	83	688
T. pyri		4		6	3	
M. occidentalis					2	24
Unknown (immatures)		1	21	4	25	18
Total phytoseiids	2	5	97	20	113	730

[1]Means ± SE

infested fields had more mites/leaf, and damage was higher on infested leaves in infested fields (these figures were not significant at $P < .05$ in 1991). Again, few predators were found (5 specimens). At preharvest, most fields had TSSM (97%), there were significantly higher ($P < .05$) densities in infested fields, and damage was significantly higher ($P < .05$) with some leaves rating 5. TSSM in four fields exceeded 10/leaf (Table 2), levels high enough to cause economic damage (pers. comm., Jim Todd, Willamette Ag Consulting, Salem, OR). However, more predators were found at this time (Table 1); most were *N. fallacis.* These predators mostly were found in three fields, with high concentrations in fields #24 and #30 (Table 2).

In 1992, TSSM were generally more dense than in 1991 (Table 1). Percent fields infested, mean number of TSSM, and mean damage levels on infested leaves in infested fields were all higher in early and mid-season. However, late-season samples were lower in all three categories than in 1991. This decline is probably due to spraying in response to perceived conditions favorable for TSSM (1992 was warmer and dryer than 1991). By mid-season, two fields had TSSM levels higher than 10/leaf, and a third had elevated levels in late-season (Table 2). Eighteen of all samples had mite levels at 1-6 per leaf; all 71 other samples were below 1 TSSM/leaf. Thus despite early and mid-season TSSM densities being significantly ($P < .02$) higher in 1992 than 1991, they posed no greater threat to the crop in 1992.

In both years, the most common phytoseiid collected was *N. fallacis.* It was the only species found in late-season 1991. *Typhlodromus pyri* Scheuten was found in early and mid-season, but was always absent by late-season. Cultural practices such as spraying may be detrimental to *T. pyri* which probably migrates into hops. *G. occidentalis* was not found in 1991, but it occurred in late-season, 1992. Its occurrence may have been related to the hot dry weather of 1992 (Croft et al. 1990).

Phytoseiids increased in commercial hops from low (very low in 1991) to substantial by late-season, especially in 1992 (Table 1). Despite some TSSM, predators were not abundant in early- and mid-season (highest level was 3.65 ± 1.57 predators/field, or 0.073 predators/leaf). At pre-harvest, predators were abundant in only two of the fields in 1991 (Table 2), but were abundant in more fields in 1992. Of nine fields where TSSM exceeded 5 mites/leaf (Table 2), five had few predators (similar to other fields with low TSSM counts), while four had some of the highest predator numbers sampled. This indicated that phytoseiids, when present in

Table 2. Commercial hop fields with elevated levels of *Tetranychus urticae* and/or *Amblyseius fallacis*.

Year	Period	Field	Mites/leaf[1]	Damage/infested leaf	Phytoseiids/leaf
1991	late	19	2.30±0.99	1.83±0.42	0.13±0.10
1991	late	24	16.91±3.15	2.74±0.18	0.69±0.24
1991	late	27	15.50±1.97	2.24±0.13	0.02±0.02
1991	late	28	19.82±4.56	2.59±0.20	0
1991	late	29	10.08±1.87	1.82±0.14	0
1991	late	30	6.40±1.88	3.04±0.15	1.2±0.22
1991	late	34	6.64±1.46	1.93±0.14	0
1992	Mid	18	20.02±4.47	2.58±0.14	0.86±0.40
1992	Mid	23	38.24±8.17	2.87±0.18	0.04±0.03
1992	Late	7	10.48±1.28	2.77±0.12	6.28±1.17
1992	Late	11	2.24+0.33	1.61+0.09	5.92+1.06

[1]Means ± SE

commercial fields, may respond numerically to TSSM. Their ability to regulate TSSM probably depends on the timing of their entry into hops.

Two fields in 1992 had very high levels of phytoseiids (Table 2). Although the cultural and pesticide histories of these fields were examined, no consistent differences were found between these fields and others which might explain the greater incidence of phytoseiids.

Escaped Hops Survey

Mite numbers were low on escaped hops in 1991 (Table 3). This season was cool and wet, which was not conducive to buildup of TSSM. TSSM numbers in 1992 started low and increased through to late-season, reaching a mean density of 1.17±.36 mites/leaf. Although this was nearly 5-fold more than in 1991, it still was a non-economic level of mites from a grower's point of view. In none of the 1991 samples did the TSSM exceed 1/leaf. In 1992, the sample with the most TSSM was 3.52/leaf. Thus it seems that favorable conditions for mites in 1992 resulted in increased TSSM over 1991 but still below those that would be of economic concern if present in commercial hops.

In both years the majority of predators found were *T. pyri,* which is a generalist feeder usually associated with rosaceous plants (Hadam et al. 1986). *T. pyri* may be a vagrant on hops as a result of its association with other mixed plants in the escaped sites, including wild blackberry or other rosaceous plants. *N. fallacis* was infrequently found on escaped hops, although it was common in commercial hops. Twenty-five *G. occidentalis* was found on escaped plants in 1992 but only 2 were found 1991, possibly because this is a dry-adapted predator (Croft et al., 1990) and 1992 was the dryer year. Nearly all *A. andersoni* found in 1992 were from a single humid site near a river; *A. andersoni* is a humidity-adapted predator (Messing & Croft, 1991). Otherwise its abundance was like that of *N. fallacis* in escaped hops. Other species were found infrequently.

Thus it appears that biological control is actively occurring on escaped hops. TSSM numbers from unsprayed sites compared favorably with those in commercial hops, in which mite control is largely brought about with pesticides. The low variation in mite numbers in escaped hops (no high peaks) compared to commercial hops indicates that biological control of TSSM may be effective and dependable.

The microhabitat and vegetation surrounding unsprayed hops varied widely, ranging from dry in full sunshine with low floral diversity nearby (*e.g.* road verges)

Table 3. *Tetranychus urticae* and phytoseiids mites found in feral hop sites.

	1991	Early 92	Mid 92	Late 92
Samples	14	13	19	16
Sample n	50	25	25	25
Mites/sample[1]	8.5±2.07	12.0±6.26	25.60±6.37	31.10±8.90
Mites/leaf	.24±.07	.48±.15	1.04±.14	1.17±.35
Phytoseiids/sample	4.7±1.28	6.38±2.87	6.74±2.27	3.19±1.29
Amblyseius fallacis	2	4	2	2
Typhlodromus pyri	58	57	32	31
Metaseiulus occidentalis	2	22	3	
Amblyseius andersoni	2	7	27	4
Amblyseius exopodalis		3		
Typhlodromus arboreus	2			
Typhlodromus mahri		2		
Typhlodromus caudiglans	2			
Unknown phytoseiids[2]	6	10	45	11
Total phytoseiids	74	83	128	51

[1]Means ± SE

[2] Unknown immatures which are unidentifiable.

to humid and shady with high floral diversity (*e.g.* forested areas next to fields). The incidence of phytoseiids and TSSM seemed unrelated to microhabitat, indicating that the microhabitat of a commercial field might be suitable for biological control of TSSM by phytoseiids.

Early Spring Survival Study

Phytoseiids (*N. fallacis*) were active and out of diapause by March 30 (Table 4), before hop vines had started growing. However, by April 13 no more were found on trap plants. Up to April 6 there was virtually no vegetation in the field, either weeds or hop vines, which is normal in overwintering hop fields. The 1991/92 winter was very warm with no prolonged frost; it seems likely that phytoseiids were active at times during the winter and early spring before plant growth occurred, feeding upon TSSM. Since there was no green matter present for spider mites to feed on, the phytoseiids may have overexploited TSSM and then starved.

Early hop leaf collections contained two *N. fallacis* females, one juvenile and several eggs found on April 6, a single female on April 13, and no predators on April 20. A few TSSM were found on the hop leaves from April 13 and 20; any predators present would probably have been associated with these TSSM. It appears that although the phytoseiids overwintered successfully, hop plants may become active too late to support early spider mite colonies required for early spring survival of phytoseiids .

Table 4. Spring trapping of overwintered *Neoseiulus fallacis* in field #30, 1992.

		PHYTOSEIIDS				
DATE	Pots	Females	Males	Juveniles	Eggs	Bean Plant Condition
March 30	2	19	0	2	Many	Dry, some green
April 6	4	6	1	0	Few	Frosted, some green
April 13	6	0	0	0	0	Frosted, some green
April 20	5	0	0	0	0	Good, slightly dry

Transect Surveys

TSSM often were present at higher densities in crops surrounding hops than in the hops themselves in early-season; they appeared to disperse into the hops as the season progressed. Three examples of this are seen in Fig. 1, all of which are from the mid-season sample period. In Field #27, no TSSM were found in hops in early-season despite levels in the adjacent strawberries of .24 TSSM/leaf, but by mid-season an edge effect was apparent (Fig. 1a). Possibly the TSSM moved into the hops on prevailing winds; both TSSM and phytoseiids are capable of dispersing on wind (Johnson & Croft, 1976; Kennedy & Smitley, 1985; Sabelis & Dicke, 1985). As the season progressed, this apparent edge effect diminished. In contrast, field #33a had a prevailing wind blowing the opposite way. Again, in early-season there were neither TSSM nor phytoseiids in the hops; by mid-season there was an apparent edge effect but at much lower numbers than Field #27 (Fig. 1b). Also, the abundant phytoseiids in strawberry never moved over into hops, despite being the highly dispersive *N. fallacis* (Johnson & Croft, 1976). The data from Field #33b indicate that the species of phytoseiid is also important in dispersal (Fig. 1c). Despite prevailing winds from the caneberries to the hops, phytoseiids were not detected in the hops. The phytoseiids found in the cane-berries were exclusively *T. pyri*, which is known to be a relatively poor disperser (Boller et al., 1988; Croft et al., 1990).

Apparently both mites and predators overwinter well in surrounding crops but poorly in hops; they then disperse into hops at rates depending on species, prevailing wind direction, and possibly other factors. Although the data in Fig. 1 are from limited sites and show considerable variability, they indicate the need for further investigation into early-season movement of predators and TSSM in relation to surrounding crops and prevailing wind direction.

CONCLUSIONS

It appears that despite intensive spraying, TSSM and their damage increase seasonally in most commercial hop fields. In six fields at pre-harvest, TSSM exceeded 10 per leaf, a large proportion of leaves had mites, and damage ratings were high. Although the economic impact of these TSSM levels needs more definitive research, an alternative management method to pesticides is desirable.

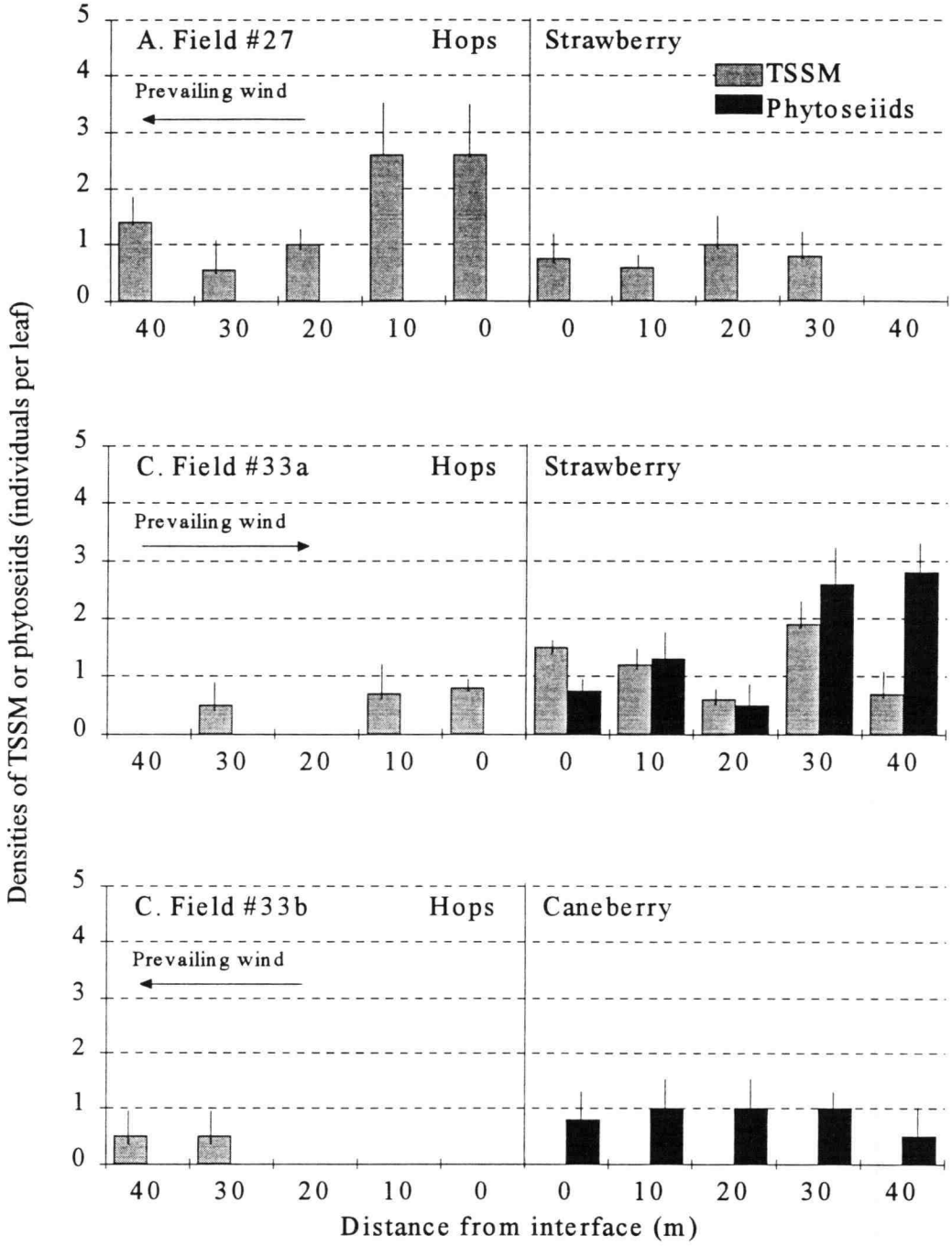

Figure 1. Levels of *Tetranychus urticae* (TSSM) and phytoseiid mites (*Neoseiulus fallacis, Typhlodromus pyri*) found in mid-season transect surveys of hop yards and adjacent crops, 1991 (lines are SE's).

Apparently biological control of TSSM using phytoseiids would be possible in hops except for 3 conditions: the limited ability of phytoseiids to establish populations in early spring, their lack of early-season dispersal into hops, and the use of cultural practices and pesticides harmful to predators. The differential early-spring survivorship of phytoseiids and TSSM makes hops similar to a perennial crop for TSSM, but more like an annual crop for phytoseiids. With their low dispersal rates into hop yards from surrounding crops, phytoseiids may need re-introduction each year. This was the conclusion of Cranham (1985) who felt that stable biological control in hops was unlikely, due to the annual nature of the crop.

The use of some cultural practices and insecticides in hop culture are difficult to avoid, but others may be modified. Planting ground covers favorable to survival of phytoseiids, and eliminating leaf stripping and hilling around hops, both of which remove leaves harboring phytoseiids early in spring may be helpful. Pesticide changes may include eliminating pyrethroids and using insecticides compatible with phytoseiids (Croft 1990). However, even with these modifications, the early spring pool of phytoseiids may be too low to ensure biological control and thus supplementary releases may be required.

Supplementary releases would be most economical when used in an inoculative manner. From these studies, the key time to release would be early spring, when TSSM start to develop but naturally-occurring phytoseiids are rare. The number of releases, release location (within and between plants) and release density of phytoseiids have yet to be determined. Results of this study indicate that four species should be tried: *T. pyri* and *A. andersoni*, found mostly on escaped hops; *G. occidentalis,* found on both escaped and commercial hops; and *N. fallacis,* found mostly in commercial hops. The other phytoseiids collected in this study were probably incidentals and are unlikely to play a major role in biological control. It is likely that *N. fallacis* and *G. occidentalis* will have the greatest commercial impact, since they were the only species that were abundant in commercial hops. A mixture of species both might be advisable. The microhabitat on a hop plant may vary from cool and humid (suitable for *N. fallacis*) at the bottom to warm and dry (suitable for *G. occidentalis*) near the top. Moreover, since the future weather conditions at the time of release are unpredictable, releasing both species might ensure control regardless of weather conditions.

3. INOCULATIVE RELEASE OF PHYTOSEIID MITES INTO HOPS

INTRODUCTION

Effective biological control of twospotted spider mite, *Tetranychus urticae* Koch, by predaceous phytoseiid mites has been demonstrated on many fruits and vegetables and some field crops (Helle & Sabelis 1985). The levels of control achieved depend on predators and prey mites having similar spatial distributions and on there being favorable ratios of predators to prey. Also, management methods used for crop pests other than mites must be nonharmful or at least selective to predator mites (Helle & Sabelis 1985, Croft 1990).

Biological control of spider mites on hops, *Humulus lupulus* L., by phytoseiid mites has not been as successfully demonstrated as on other crops (Pruszynski & Cone 1972, Cranham 1985, Campbell 1990, Mori et al. 1990). This may be partly because this system has been studied less, but several biological or management-related factors may be involved. One factor is the selection of a phytoseiid that is well adapted to hops and local conditions (Pruszynski & Cone 1973). Cultural methods such as the removal of leaves from the crown in the spring may limit predators more than pest mites. Finally, the hop plant grows rapidly. In 10 wks it expands from just a few leaves at ground level to a trellised canopy, 6 m high. This growth pattern may allow for development of dissimilar spatial distributions of mites and unfavorable predator–prey ratios on parts of the hop plant.

Here, I report on biological control of *T. urticae* on hops after inoculative release of *Neoseiulus fallacis* (Garman), *Galendromus occidentalis* (Nesbitt), *Typhlodromus pyri* Scheuten, and *Amblyseius andersoni* Chant. These mites were selected because they are endemic on Oregon hops (Strong & Croft 1993): *N. fallacis* and *G. occidentalis* mostly on commercial hops and *T. pyri* and *A. andersoni* mostly on escaped hops. These species vary in climatic preferences: *G. occidentalis* does well under semiarid conditions, *N. fallacis* and *A. andersoni* are more humid adapted, and *T. pyri* occurs under intermediate conditions (Croft et al. 1993). Species of the complex seem to act in complimentary ways. *G. occidentalis* and *N. fallacis* are oligophagous and well adapted to control *T. urticae* (Croft & Croft 1993). Both disperse rapidly (Johnson & Croft 1976, Hoy et al. 1984) and show strong numerical

responses to prey (Flaherty & Huffaker 1970a, Croft & McGroarty 1977). *T. pyri* and *A. andersoni* are more polyphagous, feeding on several arthropod species and pollen; they aggregate less and provide the best mite regulation at low prey densities (McMurtry & van de Vrie 1973, Walde et al. 1992). *T. pyri* disperses slowly but *A. andersoni* does so more rapidly over longer distances (Dunley & Croft 1990, Croft 1994).

MATERIALS AND METHODS

Four experiments were run on different commercial hop farms in the Willamette Valley, Oregon, three in 1992 and one in 1993. Tests in 1992 had an untreated check (no predator releases) and releases of *N. fallacis* alone, *G. occidentalis* alone, *N. fallacis* plus *G. occidentalis*, and a variable plot of *A. andersoni* plus *T. pyri* on experiment 1, *A. andersoni* alone on experiment 2, and *T. pyri* alone on experiment 3. All treatments were replicated four times each. The 1993 test had an untreated check and *N. fallacis* alone, *G. occidentalis* alone, and *N. fallacis* plus *G. occidentalis*, with five replicates each. Tests had completely randomized designs linearized along 1–2 rows of hops; plant spacing within fields was 2.5 by 2.5 m. Each test unit was a single hop plant near a support pole (a wooden pole supporting the wire trellis; hop plants grow up strings suspended from these wires). Test units were separated by 8–24 nontest plants (20–60 m) and the whole experiment was embedded in a buffer 30 m wide in which selective sprays were used. Diazinon was used for control of hop aphid, *Phorodon humuli* (Schrank). The *T. urticae* and phytoseiids studied here were resistant to diazinon (W.B.S., unpublished data). Propargite was used on neighboring nonexperimental plants for mite control. This miticide is moderately toxic to *T. urticae* and nontoxic to the phytoseiids (Croft 1990).

Amblyseius andersoni and *T. pyri* were reared in stock laboratory colonies. Stock colonies consisted of heavy paper surrounded by a water moat in a tray, reared at 23 °C and a photoperiod of 16:8 (L:D) (McMurtry & Scriven 1964). These species were released directly onto hop plants from the stock colonies.

Galendromus occidentalis and *N. fallacis* from stock laboratory colonies were reared on *T. urticae* on lima bean ('Henderson babybush') in greenhouses at 26:21 °C (D:N) and a photoperiod of at least 16:8 (L:D) h. Beans were planted in vermiculite

in polyethylene bags. When the first pair of leaves started to expand, plants were inoculated with *T. urticae*. One week later, beans were inoculated with predators. Two weeks later abundant phytoseiids of all stages were present, and few *T. urticae* were left on bean plants. These two predator species were introduced to hop plants on the bean leaves on which they were reared.

All releases were made from 29 April to 17 June, with three, two, four, and four releases on experiments 1, 2, 3, and 4, respectively. Adult females (25–75) and uncounted immatures and males were placed on each test unit at each release, with similar numbers in all treatments. For mixes of predators, half the number of each species was introduced. Predators always were released in the lower 2 m of plants, because plants were that short in the spring. To ensure food for predators, 10 adult female *T. urticae* per plant (plus uncounted immatures) were released once in the spring, on every plant in experiments 1, 2 and 4, and on all but untreated checks in experiment 3.

Plants were sampled every 2 wk from 27 May (1992) or 3 June (1993) until tests ended. Tests ended in experiments 1 (9 July) and 3 (7 August) because of propargite sprays and in experiments 2 (17 August) and 4 (18 August) because of harvesting. Samples were four leaves each from five plant heights (0.5, 1.5, 3, 4.5, and 6 m) from each test plant. Samples were placed in coolers for transport to the laboratory where they were stored at 2°C and observed within 7 d under a microscope at 40X. Each life stage of each species of predator and spider mites was counted. Data from each experiment and date were transformed by log (x + 1) and analyzed with a two-factor repeated measures analysis of variance (factors were treatment and plant height); means were separated with the SAS REGWQ method (SAS Institute 1987).

RESULTS AND DISCUSSION

Biological Control

Overall, some control of *T. urticae* was provided by *N. fallacis* or *G. occidentalis*, or both, in all experiments (Table 5), except with *G. occidentalis* alone in 1993. In 1992, spider mites in untreated check plots increased rapidly, but *N. fallacis*

Table 5. Mite densities (all stages) per hop leaf in four hop experiments, each with 5 predator release treatments.

A. *T. urticae*

Experiment:	1						2				
Treatment	5/27/9	6/11/9	6/23/9	7/7/92	7/21/9	8/6/92	6/11/9	6/23/92	7/7/9	7/21/92	8/17/9
Nf	0.2	3.4	6.6	8.6	26.0a	15.5a	8.8	5.2	5.9ab	7.1b	13.4a
Nf+Go	0.3	2.5	3.1	19.9	64.4bc	24.3ab	5.4	2.8	3.8a	2.7a	12.8ab
Go	2.1	6.1	3.4	8.3	53.9b	32.2b	10.9	11.8	11.8b	3.6ab	20.4b
Tp/Aa[1]	0.0	0.0	2.5	11.7	97.1c	148.9c	13.1	8.2	22.2c	5.2ab	8.8c
Control	0.8	0.7	5.6	39.7	395.4d	352.8d	3.0	10.8	68.2d	25.4c	18.6d

B. Phytoseiids[2]

Experiment:	1						2				
Treatment	5/27/9	6/11/9	6/23/9	7/7/9	7/21/9	8/6/9	6/11/9	6/23/9	7/7/9	7/21/9	8/17/9
Nf	0.0	0.0	0.7a	2.0a	3.7a	9.1a	1.6	0.5a	1.3a	1.3	1.4
Nf+Go	0.0	0.3	0.5a	1.4ab	4.0a	5.2a	1.1	0.4ab	0.9a	0.7	2.6
Go	0.0	0.6	0.6a	0.9b	4.2a	6.0a	0.5	0.6a	0.8a	0.6	1.4
Tp/Aa	0.0	0.0	0.1b	0.0c	0.1b	0.7b	0.1	0.1bc	0.3b	0.8	1.6
Control	0.0	0.0	0.0b	0.0c	0.3b	1.1b	0.0	0.0c	0.0b	1.3	5.4

Table 5. Continued.

A. *T. urticae*

Experiment:	3					4					
Treatment	5/27/9	6/11/92	6/23/9	7/7/9	7/21/9	5/25/9	6/8/93	6/21/9	7/8/93	7/27/9	8/18/9
Nf	3.9	7.6	70.4	109.6	3.6a	0.0	0.1	0.9	0.8	2.6	14.1a
Nf+Go	0.5	7.2	93.0	198.6	0.18a	0.4	0.6	0.8	1.1	1.6	12.5a
Go	7.3	34.9	13.8	191.8	2.4a	0.2	0.1	1.1	1.6	5.8	43.4b
Tp/Aa	1.7	14.2	45.3	499.3	19.3b	--	--	--	--	--	--
Control	1.0	6.2	47.0	695.3	10.7b	0.0	0.2	1.5	2.0	3.9	45.7b

B. Phytoseiids

Experiment:	3					4					
Treatment	5/27/9	6/11/9	6/23/9	7/7/9	7/21/9	5/25/9	6/8/93	6/21/9	7/8/93	7/27/9	8/18/9
Nf	0.1	0.7a	1.0a	6.5a	1.6	0.1	0.1	0.1	0.0a	0.1	0.4ab
Nf+Go	0.1	0.8a	0.8b	2.4a	0.0	0.1	0.0	0.1	0.1b	0.2	0.3ab
Go	0.3	1.2a	2.1a	9.2b	0.6	0.1	0.0	0.2	0.1b	0.1	0.9a
Tp/Aa	0.0	0.1b	0.0c	0.1c	0.2	--	--	--	--	--	--
Control	0.0	0.0b	0.0c	0.0c	0.0	0.1	0.0	0.0	0.0a	0.0	0.0b

Within a column, means followed by different letters are different ($P > 0.05$, SAS REGWQ procedure [SAS Institute 1987]). Nf, *N. fallacis;* Go, *G. occidentalis*; Tp, *T. pyri*; Aa, *A. andersoni.*

[1] Exp. 1, *T. pyri* + *A. andersoni*; Exp. 2, *A. andersoni*; Exp. 3, *T. pyri*; Exp. 4, no treatment.

[2] All phytoseiid species encountered are included in this table, regardless of the experimental treatment.

and *G. occidentalis* limited them in this warm, dry year. In some cases, predators reduced *T. urticae* by 95% over untreated checks. Compared with *M. occidentalis* and *N. fallacis*, *T. pyri* and *A. andersoni* influenced *T. urticae* much less in 1992 (Table 5A). As noted, the life histories of *T. pyri* and *A. andersoni* are more suited to keeping spider mites at low densities rather than reducing them from high densities. Spider mite densities in *T. pyri* or *A. andersoni*, or both, plots were intermediate between those in untreated checks and *N. fallacis* or *G. occidentalis*, or both, plots. Densities of all phytoseiid species were generally highest in *N. fallacis, G. occidentalis,* or *N. fallacis* + *G. occidentalis* plots, and significantly lower in *T. pyri/A. andersoni* plots and untreated checks (Table 5B).

In experiment 1 in 1992, *T. urticae* densities in *N. fallacis* and *G. occidentalis* plots were much lower than in untreated check plots on the last two sample dates, with up to a 95% reduction (Table 5A). *T. urticae* were most common in untreated checks, then *T. pyri* + *A. andersoni* plots, then *G. occidentalis* and *G. occidentalis* + *N. fallacis* plots, and least in *N. fallacis* plots. Biological control in this experiment occurred with *N. fallacis* or *G. occidentalis,* or both, but not at 5–10 spider mites per leaf, which is the current provisional action threshold. However, this threshold is based on the damage that 5–10 mites per leaf will cause at some future point if biological control agents are not present. Here, mites declined by 6 August, suggesting that >5–10 per leaf could have been tolerated. In the *N. fallacis* plots, 26.0 and 15.5 spider mites per leaf were present before harvest on 21 July and 6 August, respectively; this may have been an acceptable level of biological control. In all plots, the elevated densities of phytoseiids where either *N. fallacis* or *G. occidentalis* were released persisted until the last sample date (Table 5B).

Experiment 2 started the 1992 season with more *T. urticae* (5–15 per leaf) than the other three experiments (Table 5A). In the *N. fallacis*, *G. occidentalis*, and *N. fallacis* + *G. occidentalis* plots, *T. urticae* densities remained almost constant in time, but in the untreated check and *A. andersoni* plots, spider mites peaked on 7 July and then declined. On 7 July, *N. fallacis* and *N. fallacis* + *G. occidentalis* plots had the fewest spider mites, followed by the *G. occidentalis* plots, and the *A. andersoni* and untreated check plots had the most. On 21 July, the *N. fallacis* + *G. occidentalis* plots had the fewest spider mites, followed by the *A. andersoni, N. fallacis,* and *G. occidentalis* plots, and the untreated checks had the most spider mites. There were no differences in treatments on 17 August because of a decrease in *T. urticae* in the untreated check and *T. pyri/A. andersoni* plots. Concurrently, the differences between

treatments in phytoseiid abundance disappeared in the last two sample dates (Table 5B); this was probably caused by an influx of endemic phytoseiids (both *N. fallacis* and *T. pyri*) into the experimental plants and may have accounted for the *T. urticae* decline in untreated checks. I also saw many macropredators (mainly *Stethorus* spp. and an unidentified cecidomyiid) in this field, which could have contributed to the *T. urticae* decline. Along with these endemic predators, our released *N. fallacis* and *G. occidentalis* gave commercially acceptable control through the summer. This suggested the utility of integrating other natural enemies with the release of phytoseiids, perhaps by using selective pesticides.

Experiment 3 (1992) had so many *T. urticae* that propargite was applied (1.3 kg [AI]/ha of 25 wettable powder [WP]) on 9 July. Although the applicator tried to avoid experimental plants, the drop in spider mites in all treatments on 21 July (Table 5A) was probably from spray drift. However, significant biological control was seen in the *N. fallacis*, *G. occidentalis*, and *N. fallacis* + *G. occidentalis* plots on both 7 and 21 July. These plots had fewer spider mites than others, with up to an 84% reduction over untreated checks before the spray. Untreated check and *T. pyri* plots were not different from each other. Differences between plots persisted after spraying, which indicated the value of propargite as a selective acaricide (Croft 1990). However, differences in the abundance of phytoseiids did not persist, probably because of starvation in all plots (Table 5B). In this experiment with many spider mites, *N. fallacis* and *G. occidentalis* did not provide a high level of control, but releases still were useful when used with a selective acaricide.

Spring of 1993 was wet and cool (Fig. 2), resulting in fewer *T. urticae* than in tests run in 1992 (Table 5A). There was no strong evidence for differences between treatments until 18 August, when *N. fallacis* and *N. fallacis* + *G. occidentalis* plots had significantly fewer *T. urticae* than untreated checks and the *G. occidentalis* plots. There was weak evidence for differences on 27 July ($P = .062$) as well. This experiment had low spider mite abundance compared with experiment 3, yet predators significantly reduced spider mites in this experiment, too. This indicated that our results were not dependent on general spider mite densities.

The amount of control provided by *G. occidentalis* was nearly equal to that of *N. fallacis* in 1992, but it was inferior in 1993. As noted, 1992 had a warm dry spring (Fig. 2), during which *G. occidentalis* fared well; 1993 had a cool moist spring, which apparently was detrimental to this species of phytoseiid. This indicated that releasing

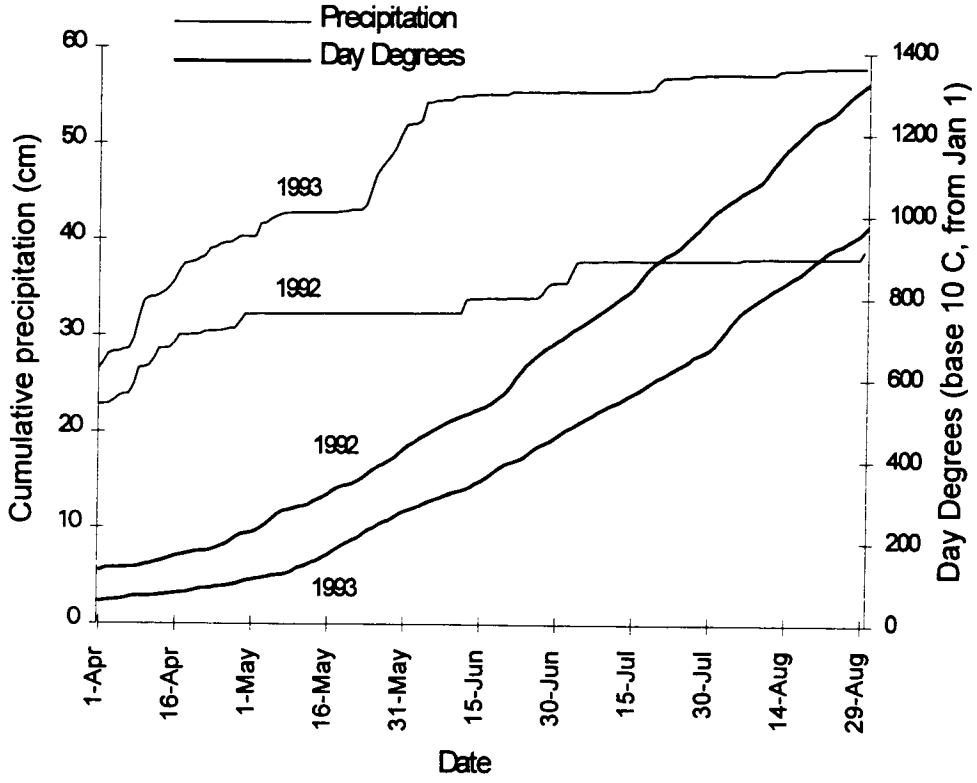

Fig. 2. Cumulative precipitation (cm) and day-degrees (base 10 °C) in 1992 and 1993 (accumulated from Jan. 1).

N. fallacis and *G. occidentalis* together may be beneficial since they respond differently to weather conditions.

Predator-Prey Ratios

I analyzed the relationship between predator/prey ratios and the success of biological control in experiments 1, 2, and 3 in 1992. Data from *N. fallacis, G. occidentalis,* and *N. fallacis* + *G. occidentalis* plots were used, and 20-leaf samples (see Materials and Methods) without prey were omitted since these resulted in predator/prey ratios of infinity. The predator/prey ratio in the second sample was compared with the number of spider mites at peak densities or the predator/prey ratio at peak spider mite densities. Data from the second sample date were used since there were often no predators or prey in the first sample. I found that the predator/prey ratio

in early season was an indicator of biological control at peak *T. urticae* densities (Figs. 3A and 3B). Higher predator/prey ratios in early season were associated with lower peak spider mite numbers ($P < .001$, Fig. 3A) and higher predator/prey ratios ($P < .02$, Fig. 3B) at peak spider mite densities. I then compared the predator/prey ratio to the number of spider mites at peak densities. Fewer spider mites were associated with higher predator/prey ratios ($P < .01$, Fig. 4). Thus not only did *N. fallacis* and *G. occidentalis* result in fewer *T. urticae*, but it appears that the higher the predator/prey ratio, the better the spider mite control achieved.

Spatial Aspects

Although *T. urticae* were reduced by *N. fallacis* and *G. occidentalis* as much as 95%, most treatments had >5-10 mites per leaf. Improved control might be achieved through better understanding of the spatial relationships between plant growth, and predator and prey mite dispersal. Hops grow continuously and rapidly, from the ground up strings to 6 m in 6 wks and then by lateral growth of flowering branches in the next 4 wk. This type of growth may provide a refugium for *T. urticae* as a predator-free space on newly formed plant parts. This has been seen on rapidly growing grape (Flaherty & Huffaker 1970b) and cucumber (Strong 1989). Success of biological control may be linked to the relative dispersal of predators and prey, which could depend upon initial *T. urticae* numbers and predator/ prey ratios in spring, at the bases of young plants. I hypothesized that if *T. urticae* densities in early season were high with a low predator/prey ratio, then *T. urticae* would rapidly disperse due to intraspecific interactions and a negative geotropic response, whereas phytoseiids would remain at plant bases because of abundant food. Poor biological control would occur, particularly at the top of plants. If early-spring *T. urticae* were scarce and the predator/prey ratio high, then *T. urticae* might move up less readily because of less intraspecific pressure, whereas the phytoseiids may disperse from plant bases more because of less food. This would result in less predator-free space and better control over the whole plant.

I found evidence of how colonization affects biological control by analyzing the distributions of predators and prey in *N. fallacis, G. occidentalis,* and *N. fallacis* + *G. occidentalis* plots in experiments 1-3. Data from experiment 4 were excluded

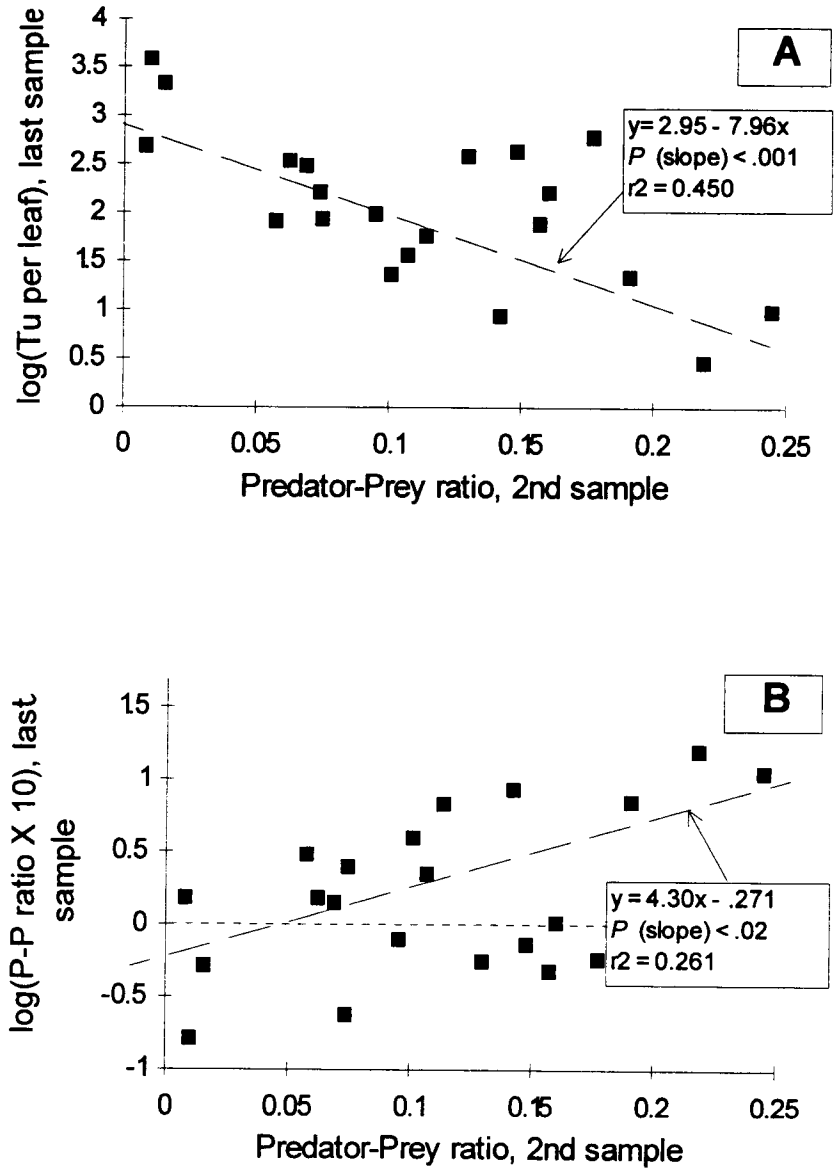

Fig. 3. Relationship between early-season predator-prey ratio and two measures of biocontrol success: (A) T. urticae per leaf at the last sample; (B) predator-prey ratio at the last sample.

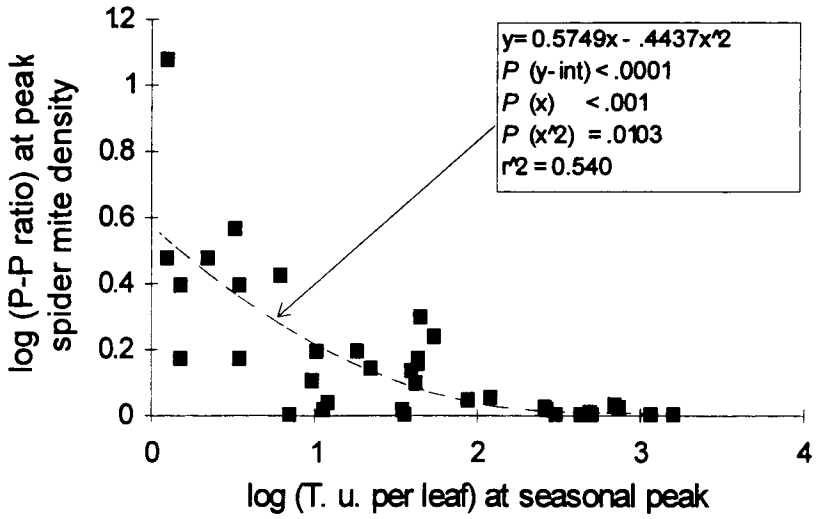

Fig. 4. Relationship between seasonal peak *T. urticae* densities and predator-prey ratios at seasonal peak *T. urticae* densities.

because there were few or no spider mites until the 3rd or 4th sample. I examined the vertical distributions of prey and predaceous mites at peak spider mite densities, and how these distributions changed over time. In preliminary tests, I found no differences in the vertical dispersions of *N. fallacis* and *G. occidentalis* (W.B.S., unpublished data), therefore data for both species were combined in the analysis presented below.

In all three experiments, *T. urticae* in the untreated check plots were most abundant in the lower or middle regions of plants (Fig. 5, right-hand side). Spider mites were scarcest in experiment 2 and in untreated checks they were concentrated at the bottoms of plants (Fig. 5A). Experiment 1 had intermediate spider mite numbers which were concentrated towards the middle in untreated check plants (Fig. 5B). The highest densities were in experiment 3, where *T. urticae* also were most common in the middle elevations of untreated check plants (Fig. 5C). Thus, it appeared that the spider mites did not concentrate in plant tops as expected. This differs from the hotter hop growing regions such as the Yakima Valley of Washington, where *T. urticae* often accumulate in tops of hops (Sites & Cone 1985).

The distribution of spider mites at low or medium densities was influenced by predators (experiments 2 and 1 respectively, Figs. 5A and 5B). *T. urticae* had a more uniform vertical distribution in treatments than in untreated checks, presumably because of predation at the plant bottoms. At high densities, spider mites were much less abundant in treatments than untreated checks, but distributions were similar (experiment 3, Fig. 5C).

In all experiments, predators were mostly found between 0.5 and 3.0 m elevations. It was useful to examine predator/prey ratios at each height as well as spatial distributions. At low spider mite densities (Fig. 5A), predator/prey ratios at the lower three plant heights were favorable at ca. 1:6, 1:4, and 1:7 for the bottom, 1.5 m, and 3.0 m heights respectively. Phytoseiid/spider mite ratios <1:10 are considered favorable in many cropping systems (Croft & Hoyt 1983; Wilson et al. 1984). At intermediate spider mite densities (Fig. 5B), ratios were less favorable at ca. 1:12, 1:6, and 1:12 at the bottom, 1.5 m, and 3.0 m hts, respectively. At high mite densities (Fig. 5C), ratios were least favorable of all, at 1:4, 1:9, and 1:37. At plant tops, predator/prey ratios also were poor between 1:14 and 1:52, regardless of spider mite abundance.

Summarizing these data, there was clear evidence of relationships between predator and prey densities and their distributions at peak *T. urticae* densities, and the extent of biological control achieved. There was only slight evidence supporting the ideas that spider mites would accumulate at plant tops at high spider mite densities, and that predator/prey ratios would be higher at tops of plants with low spider mite densities.

However, because average data from many plants were used for analysis, some within-plant interactions may have been obscured. I therefore examined data from individual plants through time to determine more specific relationships between *T. urticae* numbers and changing predator and prey densities and distributions. Three plants from experiment 3 are representative of these relationships. On plant 9 (an untreated check without predators) *T. urticae* were found in 27 May samples and they quickly dispersed up the growing plant, reaching the top by 23 June (Fig. 6A). They became abundant throughout, but were most abundant in the middle heights, with densities exceeding 2000/leaf. Propargite reduced numbers by 21 July, but the general pattern of the spatial distribution of *T. urticae* remained almost the same.

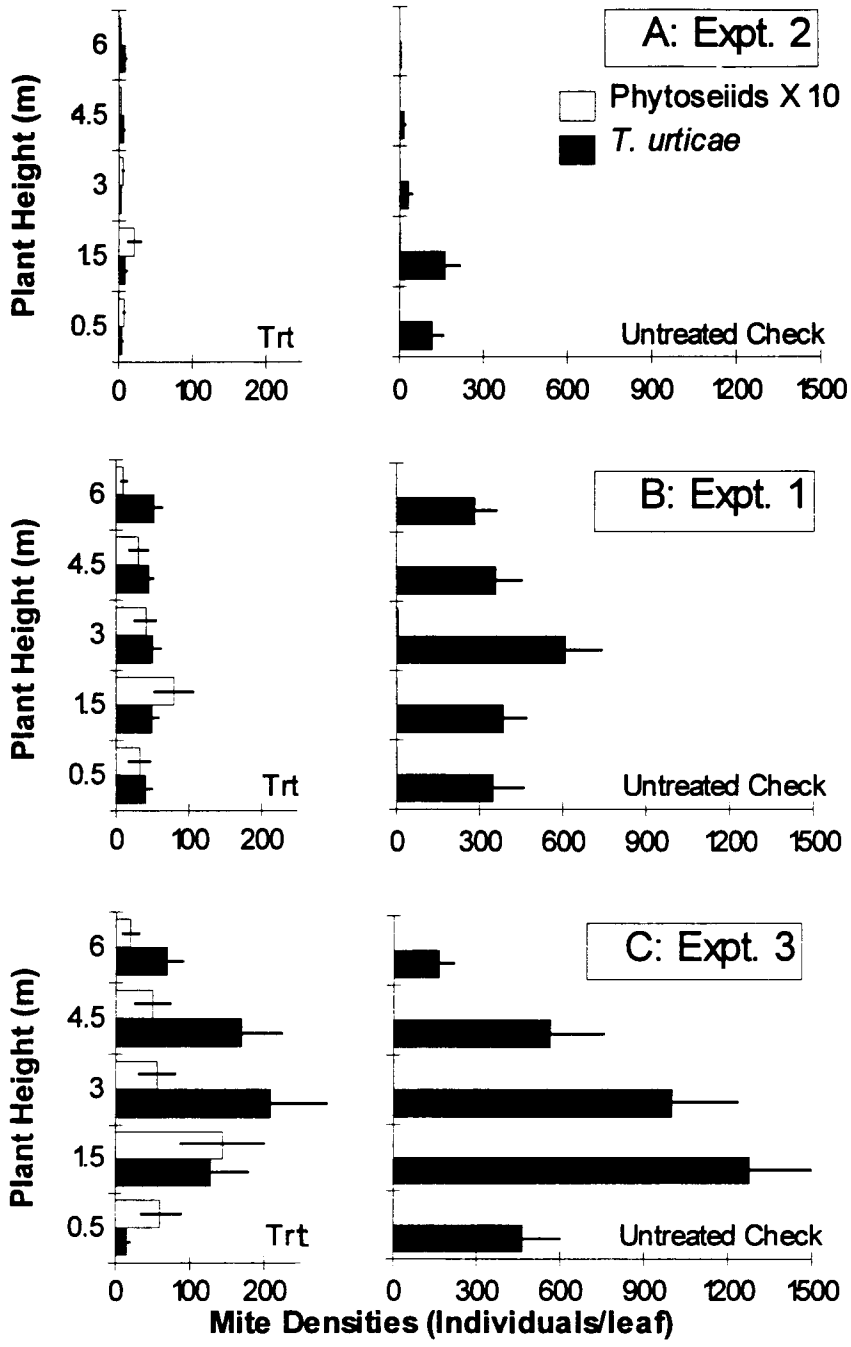

Fig. 5. *T. urticae* densities as a function of plant height at peak *T. urticae* numbers in 3 fields. (A) Exp. 2, low *T. urticae* densities. (B) Exp. 1, medium *T. urticae* densities. (C) Exp. 3, high *T. urticae* densities. Bars indicate S.E. about the mean. Trt, phytoseiid treatments exclusive of *T. pyri* and/or *A. andersoni* treatments.

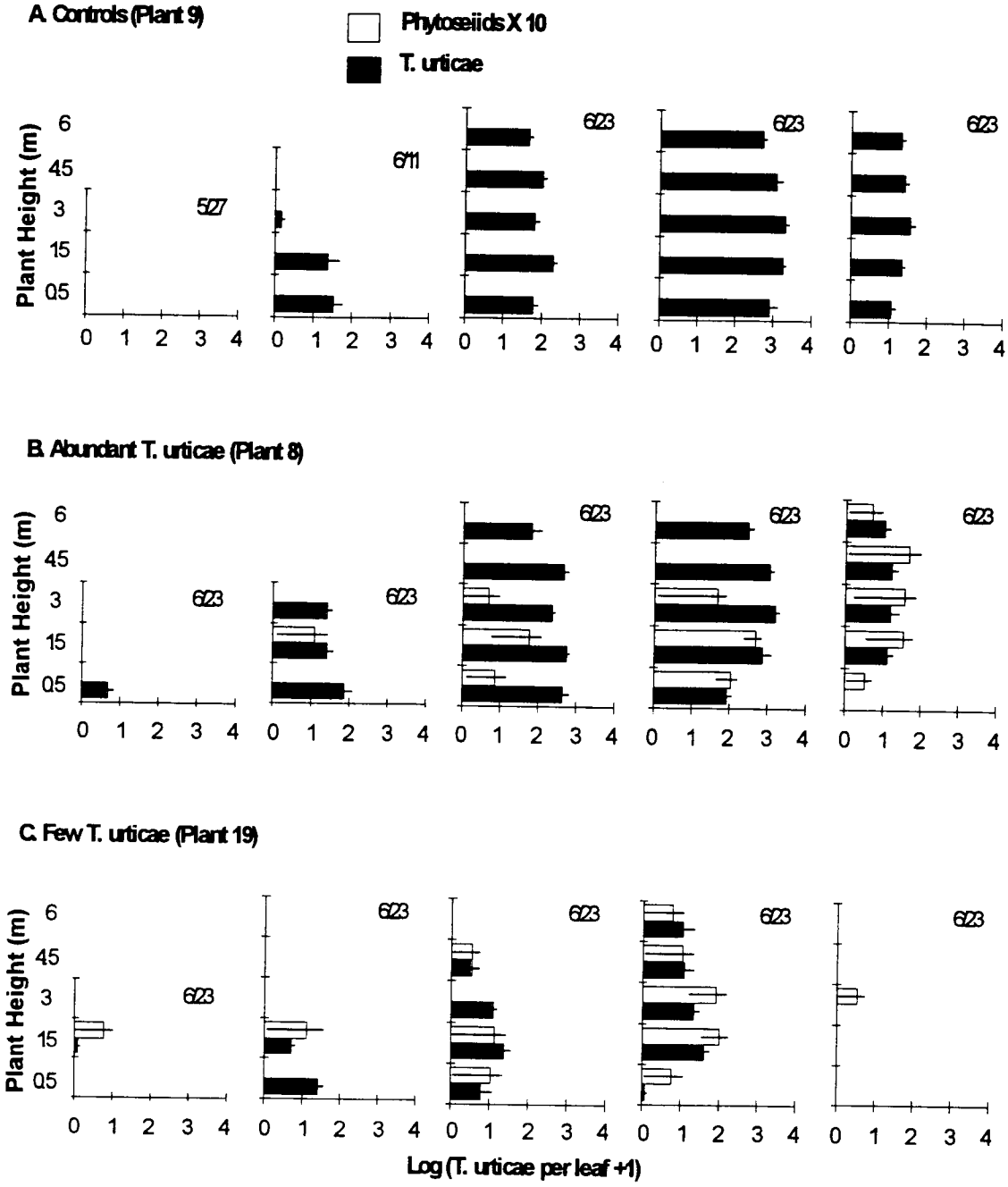

Fig. 6. *T. urticae* densities as a function of plant height through time on 3 individual plants from Exp. 3. (A) Plant 9, a control plant (no predators). (B) Plant 8, abundant *T. urticae* in early season. (C) Plant 19, few *T. urticae* in early season.

On plant 8, an *N. fallacis* + *G. occidentalis* treatment, *T. urticae* but not predators were found on 27 May (Fig. 6B). By 11 June, they moved up to 4.5 m, while *N. fallacis* were only at 1.5 m. *T. urticae* became abundant on the entire plant and reached >2000/leaf by 7 July. *N. fallacis* were limited to the lower regions on 7 July, presumably because abundant prey diminished dispersal. By 21 July, propargite reduced *T. urticae* and only then did *N. fallacis* become abundant in the upper plant areas.

Plant 19 received *N. fallacis* + *G. occidentalis*; *T. urticae* were less abundant on 27 May than on plant 8 but some predators were present (Fig. 6C). Dispersal of *T. urticae* was slower than on plant 8, and spider mites did not reach 6 m until 7 July. *T. urticae* peaked on 7 July at 51 per leaf, much lower than on plant 8. By 7 July predators reached 6 m, apparently because of higher dispersal related to lower prey densities. Propargite plus abundant predators reduced *T. urticae* to near zero and most predators dispersed or starved on hop plants by 21 July.

CONCLUSIONS

Naturally occurring biological control of spider mites is difficult on hop because this perennial is managed much like an annual: above-ground vegetation is entirely removed during winter. Such practices make it difficult to obtain long-term equilibria between predator and prey mites. In spring, other practices such as vegetation removal and non-selective pesticides are used which harm phytoseiids more than *T. urticae*. In summer, plants grow rapidly, resulting in a transient predator-free space or refugium for *T. urticae*.

Despite these constraints, our tests show that introduced *N. fallacis* and *G. occidentalis* either alone or together can reduce *T. urticae* on hops. The extent of reduction depends on initial ratios, spatial distributions, and rates of dispersal of predators and prey. Control may be improved by modifying cultural practices or manipulating early predator/prey ratios in space (distributing predators at several points on the plant) and time (releasing at different times in the season). Between-plant dispersal of predators may be important to the long-term regulation of *T. urticae* and stability of predator-prey relationships on hop. Currently, this movement probably is limited, especially in spring when predators are not abundant on upper

plant parts. A better understanding of the factors affecting dispersal and spatial aspects of the predator-prey interaction within and between hop plants may help in developing a biological control protocol for *T. urticae* on hops.

4. OPTIMAL USE STRATEGIES FOR *NEOSEIULUS FALLACIS*, PREDATOR DISPERSAL, AND POPULATION TRENDS OF PREDATOR-PREY INTERACTIONS

INTRODUCTION

Hops are attacked by several arthropod pests, the most prevalent being two-spotted spider mite (TSSM), *Tetranychus urticae* Koch, and hop aphid, *Phorodon humuli* Schrank (Campbell 1985; Cranham 1985; Neve 1991). In the past, these two pests have been controlled primarily using acaracides or insecticides, but an emerging alternative for both species is biological control using arthropod natural enemies. However, biological control on hops has not shown much commercial promise. Studies in Europe have mostly been surveys of the diversity and extent of natural enemies, with few introductions having been attempted (Aveling 1981; Ruzicka et al. 1986; Zeleny 1978; Zeleny et al. 1988). In Washington state, the phytoseiid mite *Galendromus occidentalis* (Nesbitt) was the most abundant naturally-occurring predator of TSSM (Pruszynski & Cone 1973), but in initial trials it did not control spider mites well in commercial hop yards. Releases of *Phytoseiulus persimilis* Athias-Henriot were also unsuccessful in controlling TSSM in Washington (Pruszynski & Cone 1972), but this mite showed some promise in England (Campbell 1990).

In Oregon, our research has demonstrated that TSSM in unmanaged hops are maintained at low densities, by mixed species of native phytoseiids (Strong & Croft 1993). Furthermore, inoculative release of *G. occidentalis* and *Neoseiulus fallacis* (Garman) reduced TSSM on single plants in commercial fields (Strong & Croft 1995). *N. fallacis* was determined to be the most likely candidate for use in a commercial biological control system. This phytoseiid is oligophagous (Croft & Croft 1993) with a preference for tetranychids (Helle & Sabelis 1985) and is adapted to humid conditions (Croft et al. 1993) such as found in hop growing regions of Oregon. This species reduced TSSM on individual plants by up to 90% from untreated checks, but final TSSM numbers were still higher than a provisional threshold of ca. 5-10 TSSM per leaf (Strong and Croft 1995). To be commercially acceptable, control needed to be improved so that *N. fallacis* could maintain TSSM at or below the action threshold.

To this end, we conducted research on predator release methods and cultural modifications. We also report on predator dispersal and spatial aspects of predator-prey interaction which may influence the persistence of biological control both within and between seasons.

MATERIALS AND METHODS

All tests were conducted in the Willamette Valley, Oregon in 1992-4. Tests on height of predator release, release timing, and hilling/ stripping of plants were similar in both 1993 and 1994. These three tests were conducted in a 0.4 ha experimental hop yard which was managed like a commercial yard except for insecticide and acaracide use. Diazinon and imidachloprid were applied to all plants for aphid control. Our phytoseiid predator strain of *N. fallacis* was resistant or tolerant to field rates of these aphicides (WBS, unpublished data). No acaracides were applied in 1993 since TSSM were at low levels until mid-August. In 1994, a selective acaracide, propargite, was applied to all non-test plants using a hand-held nozzle attached to a commercial high-pressure sprayer. This maintained TSSM at low densities on non-test plants.

Crowning and larger-scale predator release tests were run in commercial fields with no special management alterations. Aphids were controlled with diazinon or imidachloprid and mites with propargite or avermectin. In the crowning/overwintering survivorship studies, tests were completed by the time acaracides were applied. In the larger-scale release trials, no acaracides were applied to the area of *N. fallacis* release.

All *N. fallacis* for release were reared on *T. urticae* on lima bean (Henderson babybush) in greenhouses at 26:21 (D:N) °C and at least 16:8 (L:D) h photoperiod. Beans were planted in vermiculite in polyethylene bags. When leaves started to expand, plants were inoculated with *T. urticae*; one week later, they were inoculated with predators. Two weeks later phytoseiids of all stages were present and few *T. urticae* were left. Bean plants were then introduced with the predators to hop plants.

Predator Release Experiments

Release Height-- The site of predator release on a hop plant may be important to control success. Hops are perennials which overwinter as subterranean crowns in bare fields. Vines start growing in March, rapidly climb up strings, and reach a wire

trellis suspended 6 m above the soil surface by June. Overwintering TSSM colonize the small plants and disperse upwards as the plants grow (Strong & Croft 1993). If predators are not released near where TSSM occur, spatial disassociation and poor biological control may result. Release height treatments were: 1) predators released at the plant base only, 2) base + plant top only, and 3) at 1.5 m intervals along the plant. A check (no predators released) was included in 1994 but not in 1993. Test units were individual plants, and each test plant was separated by at least 3 non-test plants. Five replicates were used in a randomized complete block design. An equal number of predators (*ca.* 15 adult females plus uncounted immatures and eggs) were released onto each plant, but were divided along plant heights according to treatment. Plants were sampled every 2 wk by collecting 4 leaves from each of 5 heights (0.5, 1.5, 3, 4.5, and 6 m) per plant; only leaves from or near the main stem were collected. Leaves were examined with a 40X stereomicroscope and all stages of TSSM and *N. fallacis* were counted. Data were analyzed by a 2-way split-plot ANOVA for treatment and plant height and means separated by a SAS REGWQ test (SAS 1987).

Release Timing-- Since TSSM invasion of hops and their rates of numerical increase are variable, the timing of predator introductions may be important. Releasing predators too early or late may lead to temporal asynchrony and poor biological control. Release timing treatments were: a single release on May 17 or 18; 3 releases from late April-late June; 6 releases from late April-mid July; and an untreated check (no predator releases). Equal numbers of predators (ca. 20 adult females plus uncounted immatures and eggs) were released per plant, but were divided up in time according to treatment. Replicates, test design, sampling and data analysis were as with the Release Height study.

Plant Culture Factors

Several cultural procedures are used to remove excessive foliage, which reduces humidity and helps control foliar fungal pathogens on hop (Neve 1991). The following practices might be detrimental to biological control.

Stripping and Hilling-- In stripping, leaves are removed from the lower 1.5 m of plants in May; in hilling, soil is piled on the plant base in early June. We suspected that more predators than prey may be removed by either or both actions, and thus they would be detrimental to biological control. This might be more so when prey are abundant, since predators are more likely to remain at the base of the plant (from where leaves are removed), while prey disperse up the plant (Strong & Croft 1995).

Treatments were: stripping alone, hilling alone, stripping and hilling, and a check (no stripping or hilling). *N. fallacis* were released onto all test plants including the check at *ca.* 15 adult females per plant plus immatures and eggs. Replicates, test design, sampling and data analysis were as in the Release Height study.

Crowning-- New growth is removed in March to just below the soil surface level. We suspected that crowning removes overwintered predators from plants, and also depletes prey, possibly resulting in the predator starvation. We tested how crowning affects predator survival in a commercial field in 1994, on plants to which *N. fallacis* had been released in 1993. No predators were released in 1994. Plants were in a single row in a 9 ha field; each was separated from other test plants by at least 12 m. Nine plants were randomly assigned to two treatments, crowned (4 plants) and not crowned (5 plants). Test plants were crowned on March 22 at the same time as non-test plants, using a tractor-driven rotary cutter which chops and scatters plant material. In uncrowned plants, excessive vegetative was cut by hand on April 18 and replaced on the crown so that arthropods could move to surviving leaves as the cut vegetation dried. Four leaves were collected from main stem along the length of each plant on 4 dates, from 4/4-7/18, and examined for all *N. fallacis* and TSSM. The test was terminated due to an application of propargite on 7/29. Data were analyzed with a standard t-test (Steel & Torrie 1960).

Overwinter Survival-- Crowning may also affect predator persistence between years. Persistence would be beneficial in that predators would not need to be re-introduced each year. To determine predator persistence between years in hops, we surveyed commercial fields in spring, 1992 and 1993. All fields contained *N. fallacis* the previous year (at least 0.3 per leaf in August). In 1992, leaf collections were taken from a single field on 3/16 (50 leaves), 4/6 (35 leaves), and 4/13 (50 leaves). Since plants were short, all leaves were collected from within 0.5 m of the ground. Leaves were examined and all TSSM and phytoseiids were counted. In 1992 and 1993, lima bean plants were grown and inoculated with TSSM when leaves first appeared. Each bag had 6 plants, creating an attractive colonization site for *N. fallacis* (Johnson & Croft 1981). In one hop field in 1992 and 2 in 1993, bean plants were set on the ground against trellis support poles, an overwintering site for TSSM (Cone et al. 1985), and probably for *N. fallacis*. Bean plants were first set out in late March and exchanged with new ones every 7-14 days thereafter until mid-April. New bean plants were set against different poles to avoid trapping out the predators. After each change, old bean plants were examined for phytoseiids.

Larger-Scale Predator Releases

The population trends and within-season persistence of predator-prey interactions might depend upon the spatial scale of the interaction. Previous experiments have been on the scale of individual plants, but a commercial biological control program would be on the scale of whole fields. To determine population trends and within-season persistence of predators in larger-scale systems, we released *N. fallacis* into parts of two commercial fields in 1994. A rectangle of 0.4 or 0.5 ha was marked off and divided into two equal sections. Phytoseiids were released onto every plant of one half, but not the other (untreated check). Each plant received a total of *ca.* 15 (Exp. 1) or 20 (Exp. 2) adult female *N. fallacis* plus immatures and eggs, released in 3 applications on 4/21, 5/30 and 7/1 (Exp. 1) or 4/29, 5/18, and 6/8 (Exp. 2). Both fields were crowned, neither were hilled and only Exp. 2 was stripped. Predators initially were released into the lower .5 m of the plant; thereafter in the lower 2 m in Exp. 1. Since Exp. 2 was to be stripped, the last 2 predator releases were made between 1.5 and 2 m height. Acaracides were not applied to release plots or within 4 m to avoid drift, but were applied to checks on 7/29 (Exp. 1, propargite) and 7/8 (Exp. 2, avermectin). Samples were taken every 2 weeks from 5/5-8/16 from randomly selected plants along a "W"-shaped transect in each plot. From each plant, 1 leaf was collected from the main stem along each of 5 heights (0.5, 1.5, 3, 4.5, and 6 m); leaves were examined and all TSSM and *N. fallacis* were counted. Data were analyzed with a t-test for each date.

RESULTS AND DISCUSSION

Many test results seemed to depend upon the weather conditions. The weather in June and July of 1993 was cooler than normal, while 1994 was closer to the 15-year mean for the region. In cool years, TSSM develops less rapidly, and disperses up growing hop plants more slowly, than in warm years. This has implications in interpreting the results of our tests, so those conducted in 1993 vs. 1994 are discussed separately. Unless otherwise mentioned, all significant differences are at $P \leq .05$.

Predator Release Experiments

Release Height-- In 1993, releasing predators at the base only resulted in significantly fewer TSSM than the base + top or intervals treatments, or both, on 7/8, 8/10, and 8/27 (Table 6). This was probably because low TSSM densities stayed at the bases of plants in spring. Predators introduced to the higher plant areas, where few prey were found, would have starved. Plants that received all predators at the base effectively got a higher dose of predators, which caused TSSM levels to be different at the end of the season.

In 1994, there were never differences in TSSM densities between release treatments, but some treatments were different than the check on some dates. Also, no differences existed among treatments in the amount of phytoseiids found in either year. The paucity of differences between release treatments indicates that, when weather and TSSM densities are like those in 1994, within-plant placement is not important to biological control success. Height of release may be important at high TSSM densities, since predators then remain at plant bases while TSSM disperse up the plant (Strong & Croft 1995). If this had occurred in 1993 or 1994, then there may have been benefits to releasing in the tops of plants. However, such conditions are inauspicious for biological control. An early-season spray of selective acaracide, e.g. propargite (Croft 1990), could adjust TSSM to more closely resemble levels found in 1993 or 1994. Thus, the height of predator release would be less important.

Release Timing-- In 1993, releasing predators three or six times resulted in significantly lower TSSM than the check on 7/23, 8/10, and 8/27, while releasing once was no different than the check until 8/27 (Table 7). TSSM were very scarce in the spring 1993, so releasing all predators in the early season probably resulted in many starving. When predators were released over a period of time, at least some predators were introduced when TSSM started to increase.

In 1994, all release treatments were different than the check from 6/29 to 8/8, but no differences existed between release treatments. In this year of moderately abundant TSSM, release timing was not important. Apparently enough TSSM were present in early season that most predators in the single release survived, while TSSM densities were low enough that withholding predators for later release was not a problem. Timing could be critical in a year with dense early TSSM like in 1992:

Table 6. Densities (individuals per leaf) of predators and prey in the release height experiments. Within each date, numbers followed by different letters are different ($P < 0.05$).

1993

			TSSM			
Treatment	3-Jun	24-Jun	8-Jul	23-Jul	10-Aug	27-Aug
Base	0.59	1.48	2.63a	3.54	9.81a	94a
Base+Top	0.4	1.84	4.26b	4.61	12.78ab	121.51b
Intervals	0.05	1.36	0.69a	1.97	18.57b	66.66c
			N. fallacis			
Base	0.01	0.04	0.14	0.06	0.14	1.04
Base+Top	0	0.06	0.18	0.09	0.17	1.42
Intervals	0	0.03	0.06	0	0.18	1.37

1994

				TSSM			
Treatment	12-May	26-May	15-Jun	29-Jun	14-Jul	26-Jul	16-Aug
Control	0	0.13	1.01	1.61	11.14a	25.47a	8.82
Base	0.27	0.02	0.31	0.82	2.05b	11.62ab	5.62
Base+Top	0.3	0.08	0.24	0.83	3.85ab	16.13ab	4.83
Intervals	0.8	0.85	0.2	1.71	0.8b	7.92b	4.62
				N. fallacis			
Control	0	0	0	0.03	0.16	0.33	0.24
Base	0.12	0	0.01	0.06	0.26	0.48	0.73
Base+Top	0.15	0	0.03	0.17	0.29	0.58	0.57
Intervals	0.05	0	0.01	0.18	0.14	0.71	0.64

releasing all predators early (a single release) might be beneficial by establishing a high predator-prey ratio as early as possible. If releases were divided through time, the early releases might be too small to create an effective predator-prey ratio, and later ones too late to be effective. As discussed above, spraying a selective acaracide may ameliorate the situation when TSSM are very abundant.

Table 7. Densities (individuals per leaf) of predators and prey in the release timing experiments. Within each date, numbers followed by different letters are different ($P < 0.05$)

1993

				TSSM			
Treatment	25-May	8-Jun	24-Jun	8-Jul	23-Jul	10-Aug	27-Aug
none	1.65	0.09	3.24a	4.98a	8.12ab	85.1a	368.5a
1X	0.05	0.26	1.38b	4.35a	10.38a	71.42a	307.75b
3X	0	0.2	1.13b	2.37b	6.16b	23.94b	194.79b
6X	0	0.23	1.22b	1.25b	9.55ab	26.75b	140.38b
				N. fallacis			
none	0	0	0.01ab	0	0.02	0.05a	0.08a
1X	0	0	0.01ab	0	0.02	0.6b	2.05b
3X	0	0.03	0.06a	0.02	0.16	0.69b	1.93b
6X	0	0.09	0b	0.03	0.04	0.44b	2.42b

1994

				TSSM			
Treatment	12-May	8-Jun	15-Jun	29-Jun	14-Jul	26-Jul	8-Aug
none	3.9	1.81	2.27	5.69a	15.7a	40.29a	18.12a
1X	6.65	3.53	0.62	1.1b	0.68b	6.25b	6.08b
3X	0.95	2.75	2.88	1.67b	0.8b	3.75b	7.89b
6X	2.35	2.11	1.77	1.9b	0.62b	5.76b	7.13b
				N. fallacis			
none	0	0a	0	0.02a	0.15	0.16	0.58
1X	0.05	0.85b	0.39	0.14ab	0.16	0.4	0.51
3X	0.2	0.35ab	0.31	0.44bc	0.51	0.46	0.69
6X	0.1	0.43ab	0.31	0.48c	0.19	0.40	0.64

Plant Culture Factors

Stripping and Hilling-- In the 1993 stripping/hilling tests, plants which were hilled did not have different TSSM levels than the check, while stripping and stripping + hilling resulted in significantly more TSSM on 7/30 and 8/18 (Table 8). On 8/18, stripping + hilling had higher TSSM densities than stripping alone. In 1994, there were no significant differences between treatments, but the data had the same trends

Table 8. Densities (individuals per leaf) of predators and prey in the stripping/hilling experiments. Within each date, numbers followed by different letters are different ($P < 0.05$)

1993

	TSSM			
Treatment	25-May	2-Jul	30-Jul	18-Aug
None	0.25	0.1	0.16a	5.92a
Strip	0	0.99	2.61b	15.11b
Hill	0.55	1.25	0.5a	4.96a
Both	0	1.04	2.23b	49.23c

	N. fallacis			
None	0.1	0	0	0.24
Strip	0	0.07	0.01	0.32
Hill	0.05	0.14	0.07	0.26
Both	0.15	0.05	0.02	0.36

1994

				TSSM			
Treatment	12-May	26-May	15-Jun	29-Jun	14-Jul	26-Jul	16-Aug
None	1	0.5	0.26	1.18	1.69	11.26	9.25
Strip	0.45	2.42	0.21	0.55	0.17	10.37	11.04
Hill	2.95	1.74	0.25	0.74	3.71	13.14	12.94
Both	0	0.08	0.42	0.69	2.59	29.18	13.33

				N. fallacis			
None	0.1	0.18	0.05	0.3	0.27	0.45	0.6
Strip	0.15	0.18	0.07	0.28	0.27	0.42	0.29
Hill	0.2	0.06	0.03	0.14	0.08	0.36	0.64
Both	0	0.03	0.05	0.1	0.38	0.61	1.07

as in 1993, at least in the last two samples. Alternatively, the only differences detected in phytoseiid densities were in 1994, when there were significantly fewer phytoseiids on 5/12 and 5/26 in the stripping + hilling treatment than the other treatments. Thus it appears that these two cultural procedures can be detrimental to biological control. This may be particularly true if phytoseiids are released only in the lower portions of plants during a year of dense spider mites. In this case, the predators would remain near the plant base (Strong & Croft 1995) and discarding the lower

leaves would remove a disproportionately high number of predators, in conditions when this is least desirable. Although these cultural procedures may be important in the control of fungal diseases such as downy mildew (Neve 1991), eliminating them might help ensure the success of a biological control program for spider mites.

Crowning-- In the crowning test, there were no significant differences in phytoseiids in the first sample, but in the next two there were more phytoseiids and fewer TSSM in uncrowned than crowned plants (Fig. 7). The lack of difference on 4/4 is probably an artifact of presenting data as individuals per leaf. Crowning removes all vegetation from a plant; on 4/4 only a few leaves had regrown on crowned plants, but lush growth with >150 leaves existed on uncrowned plants. The total number of predators found was much lower on crowned than uncrowned plants. When the foliage of uncrowned plants was trimmed and replaced on the plant, predators were concentrated on the remaining leaves, resulting in the highly significant difference on 5/5. Predator densities had become equal by 18 July, but early-season interactions are the key to successful biological control, and this would be the period which crowning affects control most critically. However, this may be irrelevant in commercial fields, most of which have few phytoseiids (Strong & Croft 1993) and presumably very few in early spring. If a field did harbor phytoseiids the previous year, one might clip the foliage and replace it on the plant as an alternative to crowning.

Overwinter Survival-- The number of phytoseiids collected declined from late March to mid April (Table 9). Leaf collections (Table 9A) showed a decline of adults, immatures and eggs. The first sample was taken before crowning, subsequent ones after. Seven phytoseiid adults and several immatures and eggs were found on 3/21; phytoseiids were still present after crowning, but levels declined by 4/13. In part, dilution as the plant grows might have caused the decline, but these samples occurred at a cool time of year, when plant growth was not rapid. Bean trap plants indicated a similar trend in phytoseiid numbers in both years (Table 9B). With the first sample in both years, bean plants were placed into the field before crowning and exchanged shortly afterwards; later samples were all after crowning. Abundant phytoseiids were caught in late March before crowning, but catches declined to zero by mid-April. There may have been a decrease in the attractiveness of TSSM-infested bean plants as compared to the young hop plants at this time, but hop foliage was not dense, and few TSSM were found on it. Phytoseiid starvation might provide a better explanation. Crowning hops removes all vegetation and scatters phytoseiids and

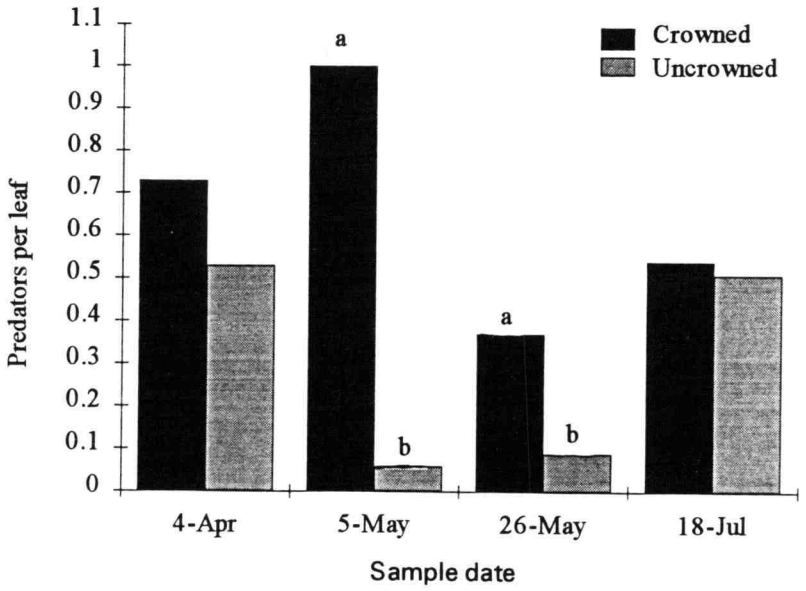

Fig. 7. Phytoseiid densities in the crowning experiment. Columns within a date topped by different letters are different ($P < 0.01$).

TSSM. A few of both probably relocate to the regrowing hop, but phytoseiids might quickly overexploit the few TSSM and subsequently starve. This would explain why some phytoseiids were found even after crowning, but numbers declined over time. Thus it appears that predators can successfully survive the winter in a commercial hop field, but crowning is a cultural barrier to predator survival into the next growing season.

Larger-scale Predator Releases

There were significant differences between release plots and checks on 7/6-8/16 (Table 10), with TSSM in release plots never exceeding 5 per leaf and TSSM in checks reaching almost 70/leaf. This occurred despite sprays of acaracides to check plots. The phytoseiid densities in early season reflected release treatments, with significantly more found in release plots until 7/6 in Farm 1 or 7/18 in Farm 2. After this, significantly more were found in non-release plots. This is probably because of dispersal of introduced predators and naturally-occurring phytoseiids (primarily

Table 9. Phytoseiids collected in early season from hop fields. A, collected from hop leaves; B, collected from bean plants placed in hop field.

A. Leaf Collections

Date	Number of leaves	Adults	Immatures	Eggs
3/21/92	50	7	2	12
4/6/92	35	2	0	3
4/13/92	50	1	0	0

B. Trap Plant Collections

Date	Sample number	# pots	Adults	Immatures	Eggs
3/30/92	1	4	19	2	25
4/6/92	1	4	7	0	4
4/13/92	1	6	0	0	0
3/25/93	2	3	14	0	12
3/25/93	3	4	8	0	9
4/2/93	2	3	2	1	0
4/2/93	3	4	1	0	2
4/8/93	2	3	0	0	0
4/8/93	3	4	2	0	0
4/15/93	2	3	0	0	0
4/15/93	3	4	0	0	0

Typhlodromus pyri Scheuten) into the non-release plots by 7/6. By this time, TSSM were abundant in the non-release plots, allowing rapid numerical response of the newly-arrived predators, which soon became significantly more abundant than the phytoseiids in the release plots. Apparently this interaction occurred too late, though, to control the TSSM in non-release plots, and TSSM there became very abundant. Naturally-occurring phytoseiids have been recorded before in commercial fields (Strong & Croft 1993, Pruszinski & Cone 1973), but they seemed to arrive too late to prevent outbreaks of TSSM. These data support that conclusion. However, our early-season introductions of phytoseiids did maintain TSSM at low densities through the growing season.

The predator-prey interaction persisted until the end of the growing season in 1994, but it is uncertain whether persistence would be a general case in the hop biological control system. If the system were not persistent within a season, then

Table 10. Densities (individuals per leaf) in the small-scale commercial release trial. Significance indicated by * ($P <= 0.05$) or ** ($P <= 0.01$).

Farm 1		TSSM		Phytoseiids	
	Date	No Release	Release	No Release	Release
	21-Apr	0	0	0	0
	10-May	0	0.04	0.04	0.04
	26-May	0.68	0.23	0	0
	24-Jun	2.22	0.88	0	0.31
	6-Jul	5.98	0.64**	0.06	0.36*
	18-Jul	31.96	2.14**	0.96	0.16*
	2-Aug	52.14	2.78**	3.64	0.26**
	16-Aug	15.28	2.28	2.34	1.22

Farm 2		TSSM		Phytoseiids	
	Date	No Release	Release	No Release	Release
	5-May	3.00	3.48	0	0.08
	18-May	0.52	0.32	0	0
	8-Jun	3.40	2.67	0	0.13
	24-Jun	3.67	1.98	0.02	0.31**
	6-Jul	14.68	2.92**	0.12	0.43
	18-Jul	24.16	2.00**	0.04	0.50**
	2-Aug	23.53	4.86**	1.80	0.82*
	16-Aug	67.04	2.48**	6.08	0.88**

predators would need to be re-introduced periodically, and the chance of TSSM outbreaks would be increased. An indication of the generality of persistence might be derived by analyzing the dispersal patterns and population trends observed in our larger-scale release tests. Phytoseiids were released at discreet points in time and space in each field. To discover TSSM colonies remote from the points of introduction, predators needed to disperse within and between plants. Within-plant dispersal of phytoseiids and TSSM on hops has been explored previously (Strong & Croft 1995). In the next section we analyze interplant dispersal and population trends of phytoseiids in hop fields.

Predator Dispersal and Population Trends

Interplant Predator Dispersal-- The quantity of basal vegetation on hop plants appears to affect interplant dispersal of phytoseiids. Phytoseiids disperse

aerially (Johnson & Croft, 1976), and diminish exponentially with distance from the source (Johnson & Croft 1981, Hoy et al. 1985). As they leave a source plant they fall downward through the air, eventually landing either on another plant or on bare soil. If they land on soil, becoming airborne again or walking to a plant is unlikely, so some individuals are lost to the system. The chance of landing on a hop plant is partly dependent upon the size of the sillouhette of adjacent plants. If these plants have been stripped and hilled, there is a very small "landing pad", and the likelihood of being lost is high. Reduced vegetation management would result in a larger landing pad and greater probability of alighting on a plant. We had preliminary results (WBS, unpublished data) which indicated that phytoseiids disperse readily from hop plants. They dispersed up to 5 rows (10 m) downwind (in the direction of the prevailing winds), but only 1 row (2 m) upwind, by 7/6. In fields with larger landing pads, dispersal distance was greater than in fields with smaller landing pads.

Population Trends-- These dispersal characteristics could have influenced the persistence and stability of population trends in the larger-scale commercial releases. If a region ("patch") has no phytoseiids, and TSSM locates the patch and starts to increase, phytoseiids could disperse from nearby plants to colonize the local outbreak. In a sequence of events typical of phytoseiid/tetranychid interactions (Sabelis & Van der Meer 1986), the phytoseiids would then overexploit the TSSM and drive them to extinction. The phytoseiids would then disperse or starve to extinction themselves, leaving the patch empty for recolonization by TSSM and then phytoseiids, starting the cycle over again. This constantly shifting mosaic of predators and prey would resemble metapopulation dynamics (Hanski & Gilpin 1991, Taylor 1991), in which habitat patches undergo cycles of colonization and extinction of predators and prey, but the interaction persists over a large area. Phytoseiid-tetranychid interactions are typically unstable on small spatial scales, with the phytoseiids overexploiting prey and extinction of both species occurring (Diekman et al. 1988, Sabelis & Laane 1986). Theoretical studies indicate that on large spatial scales, these locally unstable predator-prey interactions can be regionally persistent and stable (DeAngelis and Waterhouse 1987, den Boer 1968, Jansen & Sabelis 1992).

If mite dynamics are driven by these local extinction and recolonization phenomena, then we might expect persistence in large-scale applications. Metapopulation dynamics have 4 main characteristics (Diekman et al. 1988, Nachman 1988, Taylor 1988): empty patches (refugia for prey), asynchrony between subpopulations, extinction of some subpopulations, and dispersal of predators and

prey between patches. We tested for each of these with our data from the larger-scale predator releases. We considered patches to be either individual leaves or whole plants. A patch is defined as the habitat unit on which daily interactions occur (Hanski & Gilpin 1991); dispersal within a patch occurs routinely and entails little risk, and dispersal between patches occurs relatively rarely and entails a high risk of mortality. We restricted our analysis to samples from July 6 through August 16, since it was during this period that significant differences existed between the release and check plots, i.e. biological control was under way. Only plants from the release plots were analyzed.

1) Empty patches. The proportion of all patches (leaves or whole plants) which are empty or occupied are shown in Fig. 8. Although our method of sampling whole plants may not have detected TSSM at very low densities, the data indicated that empty patches existed at both spatial scales. The proportion of empty patches also showed no trends over time, indicating that as existing empty patches were colonized, new empty patches were being created. Fewer whole plants were unoccupied than individual leaves. The rapid growth features of hop provide a constant source of new, uncolonized leaves. These new patches are available as refugia for colonization by dispersing TSSM. However, it was older leaves from the main stem which composed our samples, suggesting that local extinctions were responsible for the creation of newly empty patches. With either mechanism (new leaves or extinction), empty patches may allow for regional persistence and stability of biological control in the hop field.

2) Asynchrony between subpopulations. Asynchronous development of subpopulations prevents in-phase oscillations across large spatial scales, thereby promoting regional stability (Nachman 1988, Sabelis and Laane 1986). The interactions of subpopulations in phytoseiid-tetranychid systems are characterized by a predictable sequence of events (Sabelis & van der Meer 1986): the prey found a colony in an empty habitat patch and begin to increase numerically; the colony is discovered by phytoseiids which then begin to increase numerically; phytoseiids overexploit the prey which decline and go extinct; and phytoseiids then disperse or starve out and go extinct in that patch. If the local interactions in a hop field are progressing synchronously, then most patches in the field should move together through this sequence of events. If the local interactions are asynchronous, then all stages of the interaction should be represented at any given time, and no trends or sequence should be obvious. We analyzed the individual patches (leaves or plants) in

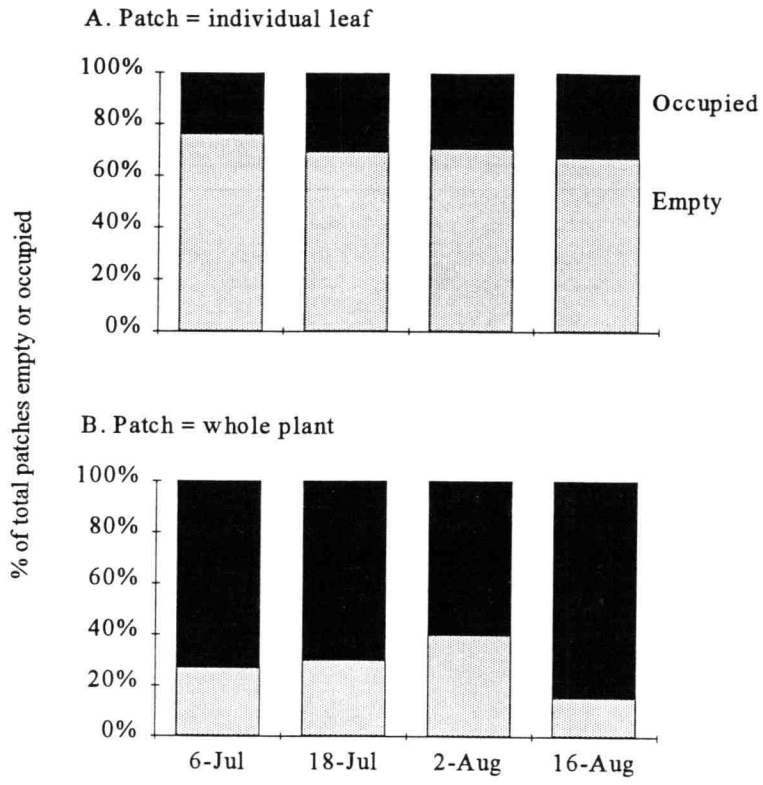

Fig. 8. Proportion of patches in larger scale release plot which are empty or occupied.

the larger-scale release trials by classifying them into 5 states and comparing the proportions represented by each at any given time. The classes were: 1) empty patches, 2) prey alone were present, 3) predator:prey ratio < 1:3, 4) predator:prey ratio > 1:3, and 5) predators only were present. These classes are meant to represent the sequence of events in development of a local interaction. A 1:3 ratio was chosen to discriminate between early and late interactions where both predators and prey were found.

We found all classes present at each sampling session (Fig. 9A and 9B), except on 8/2/94 when no plants with prey only were found. There were also no obvious trends, through time, in the proportion of patches in any occupancy class. These data are contrasted with those of Croft & Barnes (1971) concerning the control of *Tetranychus mcdanieli* McGregor by *G. occidentalis* on apple (Fig. 9C). This data set is from a similar seasonal period and had similar conditions of predator and prey

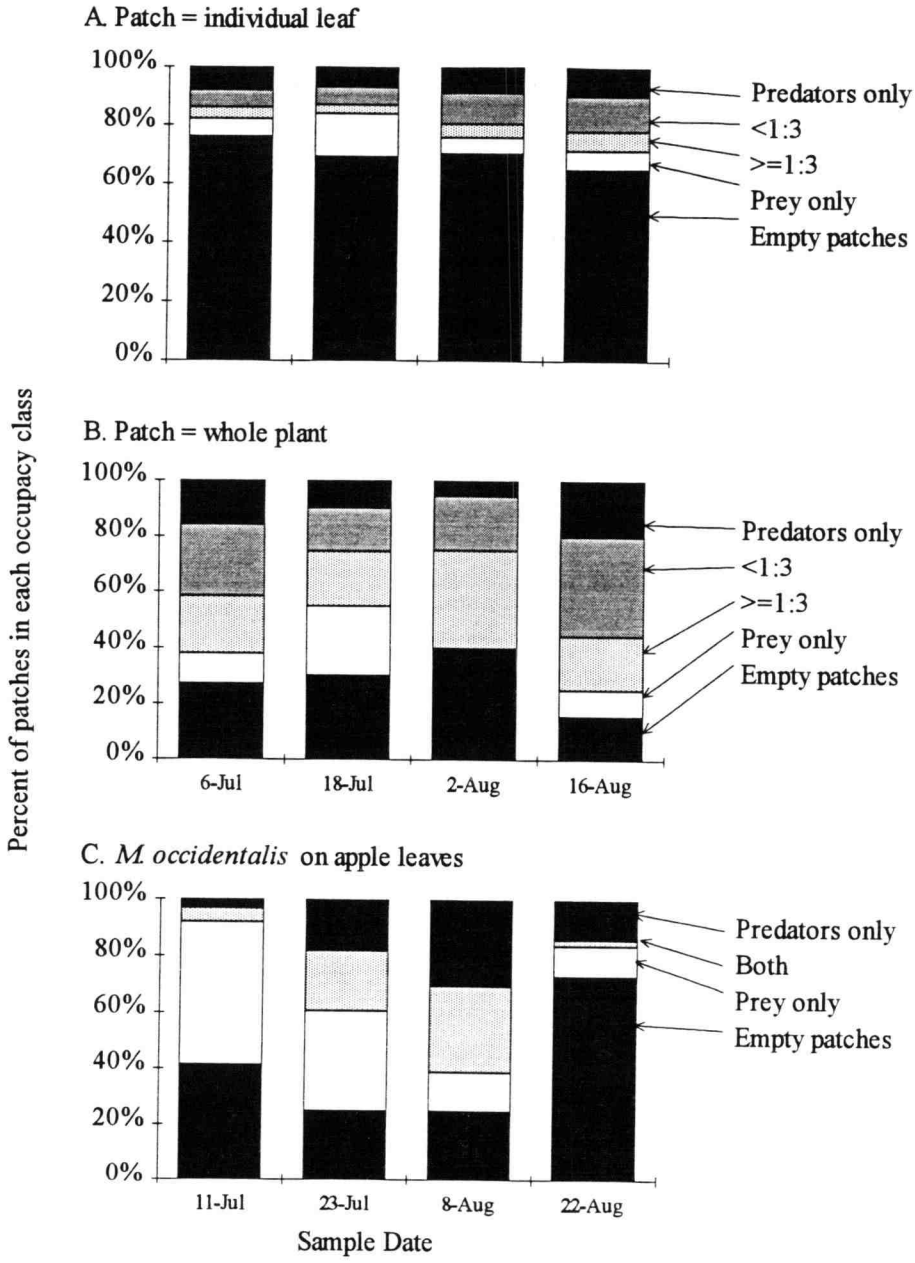

Fig. 9. Occupancy classes of occupied patches in larger-scale release plots.

densities. Abundant empty patches existed early in the interaction; they declined as the patches with prey only increased. Patches with predators only then started to increase, and finally empty patches increased again as extinction occurred. The whole field underwent a more synchronous sequence of events. The lack of this obvious

sequence in the hop system, whether a patch is considered an individual leaf or a whole plant, indicates that the subpopulations are more asynchronous in their development. This asynchronicity suggests that the system would be predictably stable and persistent within a season.

3) Extinction of some subpopulations. Our sampling did not track individual patches through time, so direct observations of extinction were lacking. However, we frequently observed leaves on which there was evidence of a recent interaction: webbing, dead TSSM corpses, cast predator skins, and sometimes predator eggs and larvae. The lack of extant arthropods, or the presence of only predator eggs or larvae (which would soon die without prey), indicated that extinction had occurred in that patch. Local extinction maintained some patches in an empty state, thus providing refugia for TSSM.

4) Dispersal of predators and prey between patches. Previously published trials indicate that within-plant dispersal occurs readily for both phytoseiids and TSSM (Strong & Croft 1995). Prey move up plants in advance of predators; the difference in rates depends on predator-prey ratios and absolute prey densities on the hop plant. Interplant dispersal has also been observed, as discussed in this paper. Data indicated that *N. fallacis* dispersed from source plants to adjacent plants, but not in high numbers early in an interaction. The latter is important because dispersing too readily or successfully could blur the boundary between patches and result in one large homogeneous population rather than a network of loosely connected subpopulations (Jansen & Sabelis 1992, Taylor 1988). This could lead to synchronization of predator-prey interactions over the entire area and large oscillations throughout the hop field, in other words a lack of regional stability and possibly persistence. Our data indicated that patches were poorly connected by dispersal, suggesting a potential for regional persistence.

It appears that the 4 conditions (empty patches, asynchrony, extinction, and dispersal between patches) were met and that patch dynamics with local extinctions and recolonizations drive our biological control system. If so, we may reasonably expect that the system will persist within a season, at least on this spatial scale. Our trials were small (predators were released on 0.2 ha, or ca. 350 plants), yet our results indicated persistence and regulation of TSSM at low densities (Table 10). The expectation of within- and between-season persistence and stability, under varying climatic conditions and on a commercial scale (up to 15 ha fields), remains to be fully tested.

5. SUMMARY AND CONCLUSIONS

Biological control of TSSM on commercial hops using phytoseiid predatory mites was determined to be feasible by studying both commercial and escaped hops. Of several species of phytoseiids found, *T. pyri* was the most common on escaped hops, occurring in most samples. A uniformly low level of TSSM regardless of location, date, or year indicated that biological control was occurring on these uncultivated hops, probably by phytoseiids.

N. fallacis was the most abundant in commercial hops, but was found in relatively few fields. It seems that some cultural activity, possibly the use of non-selective pesticides, was limiting the development of phytoseiids in cultivated hops. *N. fallacis* was probably the most common species where it did occur because of its high dispersive capabilities (Johnson & Croft 1981) and widespread pesticide resistance (Croft 1990). I felt that the microhabitat of a commercial hop field was not a constraint, in view of the broad microhabitat diversity of the escaped hops sampled, and the apparent lack of association between phytoseiid or TSSM incidence and escaped hop microhabitat.

Preliminary evidence suggested that phytoseiids overwintered in hop fields, but did not survive the early spring period. Also, they do disperse into fields from surrounding crops, but at a low rate and in the direction of the prevailing winds. Therefore it will probably be necessary to introduce phytoseiids inoculatively into each hop field at the start of each year.

I next studied four of the species of phytoseiids found to determine which would be most suitable for a biological control program in commercial hops. After releases, *T. pyri* and *A. andersoni* usually disappeared and could not be located again. These oligophagous species are not highly density-dependent, and although they may be able to regulate TSSM at low prey densities, they are unlikely to reduce burgeoning prey populations (Croft 1994, Croft & Croft 1993). Therefore they were not considered for further use in the hop biocontrol system. In 1992, *N. fallacis* and *G. occidentalis*, or both together, reduced TSSM by up to 90% from untreated checks. In 1993, *N. fallacis* was also successful in reducing TSSM, but *G. occidentalis* was not. The latter predator is adapted to dry conditions (Croft et al., 1993); 1992 was an unusually warm and dry year in the Willamette Valley, while 1993 was unusually cool and humid. *N. fallacis*, being adapted to more humid conditions, was successful in

both years. Although I at first suspected that a mixture of *N. fallacis* and *G. occidentalis* would best provide control in a variety of weather conditions, these data indicate that *N. fallacis* alone is sufficient.

An analysis of the spatial distributions and within-plant dispersal of phytoseiids in this rapidly-growing plant indicated that in conditions of low TSSM densities, the predators readily moved to the tops of plants in search of prey. However, when TSSM were abundant, there were sufficient prey at the plant bases that the predators dispersed more slowly, and were restricted to the bases of the plants where they first occurred (or were released). Thus there was an apparent limitation on biological control, resulting from the inability of predators to disperse from the bases of plants under high TSSM densities. However, this situation existed under very high TSSM densities (over 200 TSSM/leaf); later research has shown that under conditions more likely to be encountered in commercial fields (densities <100/TSSM leaf), the predators do disperse rapidly up the plant as it grows.

In order to answer questions about the management of *N. fallacis* in commercial hop fields, I conducted several studies in 1993-4. I found that the location on the plant where phytoseiids were released played very little role in the outcome of biological control, at least in the low to moderate TSSM densities encountered in 1993-4. Predators could thus be introduced into a field by hand without special machines or techniques. The timing of release was important, though; under low TSSM densities, predators should be released later (earlier releases starved out), while predators should be released earlier with high TSSM densities to ensure an adequate early-season predator-prey ratio. Since TSSM conditions are hard to predict in very early season, I recommend releasing some predators shortly after crowning (in mid April), then basing future releases upon monitoring results.

The cultural techniques of hilling, stripping, and crowning were also detrimental to biological control. Hilling and stripping, especially in combination (the normal cultural practice in the Willamette Valley) removed more predators than TSSM from the plants, resulting in poor biological control compared to untreated checks. Stripping removed overwintered phytoseiids from the hop crowns, and also reduced prey densities enough that starvation of a majority of predators resulted. Although not tested experimentally, I suspect that the common practice of maintaining bare soil through spring is also detrimental to biological control, since no reservoir of alternative prey is available for predator exploitation. This might result in large population oscillations, with extinction of the phytoseiids a possibility.

Larger-scale releases (0.5 ha) of *N. fallacis* resulted in significantly lower TSSM densities as compared to control plots. In the release plots, TSSM were maintained at commercially acceptable levels of 5/leaf or below throughout the season. An analysis of population trends, empty habitat patches, and dispersal indicated that the phytoseiid/TSSM system behaved as a metapopulation, characterized by local extinctions and recolonization of habitat patches. Theory suggests that locally unstable systems (such as the phytoseiid/TSSM system studied here) can be persistent if they behave as a metapopulation (Hanski & Gilpin 1991). Therefore I project that this biological control system will be persistent at least within the scope of a single season.

In conclusion, all indications are that *N. fallacis* will be a commercially effective biological control agent against TSSM in hops in western Oregon. In view of its humid-adapted nature, this situation may not apply to more xeric growing regions such as Washington and Idaho. The results of this research effort may be applicable in other parts of the world such as western and central Europe, Japan, and Tasmania (Barth et al. 1994), where more humid conditions prevail.

There appears to be inherent limitations to the extent of biological control achievable in hops. The rapid plant growth creates a continuous supply of predator-free leaves, possibly disrupting the spatial association between predators and prey. Although a perennial, the annual growth habit of hops disrupts continuity between seasons, which might necessitate spring predator introductions. The clean-culture methods currently practiced by farmers, in which little or no vegetation is present between fall and early summer, probably exacerbates the seasonal continuity problem. Bare soil does not allow for the development of reservoirs of alternative prey, either, and it may impose limitations to the early spring interplant dispersal of predators when hop plants are still very small. Finally, some cultural practices which are used for other horticultural purposes (control of excessive hop growth and foliar diseases) may be incompatible with biological control using phytoseiids.

In the future, biological control will need to be tested on whole fields to ensure that the system behaves similarly on this larger spatial scale. To guide management efforts accurately, an improved understanding of the spatial aspects, predator-prey population dynamics, inter- and intra-plant dispersal, and the factors affecting system stability will be needed. Modified cultural techniques such as the use of ground covers or reducing crowning, striping and hilling must be explored. And, to be truly an

effective program, biological control for hop aphids, the other key hop pest in Oregon, must be developed and integrated into the hop culture system.

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