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Title: Arthropod Community Organization and Development in Pear

Abstract approved: Redacted for privacy

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Arthropod communities in pear are conceptualized as hierarchically organized systems in which several levels of organization or subsystems can be recognized between the species population level and the community as a whole. An individual tree is taken to be the community habitat with arthropod subcommunities developing on leaf, fruit and wood subcommunity habitats. Over a hundred species are reported to colonize one or more subcommunity habitats. Each subcommunity is composed of trophically organized systems of populations. Each system of populations is comprised of a guild of arthropods that use the habitat primarily for feeding but also for overwintering or egg deposition, and associated guilds of specialized predators, parasitoids and hyperparasitoids. Understanding community organization entails understanding how subsystems and their environments interact so as to be incorporated into a unified whole. Along with the relatively specialized interrelationships so important in organizing systems of populations, higher level community subsystems are coupled through the activities of phytophagous and predaceous generalists which feed in or take their prey from more than one subcommunity. In meeting the habitat requirements of each of its life history stages, several members of the pear community move from one subcommunity to another during the course of community development and serve to integrate these subsystems. Additional habitat, trophic and life history aspects of subsystem incorporation and interpenetration are discussed.

Community development or change in organization through time is conceptualized as being jointly determined by the development of the habitat and the organization of the species pool. Seasonal development of the pear arthropod community is described in terms of changes in the species composition, size, and spatial distribution of guilds and subcommunities. Community habitat development is taken to be the primary determinant of changes in community structure and organization. As the season progresses, changes in the kinds and biomass of developmental states of each subcommunity habitat are accompanied by changes in the kinds, number or biomass, and distribution of associated community subsystems. Although the influence of habitat development on community development is emphasized, it is from the the species pool that arthropods colonize pear. The species that colonize, and their abundance and time of arrival is partially determined by the organization of this system of communities.

Arthropod Community Organization and Development in Pear

by

Larry J. Gut

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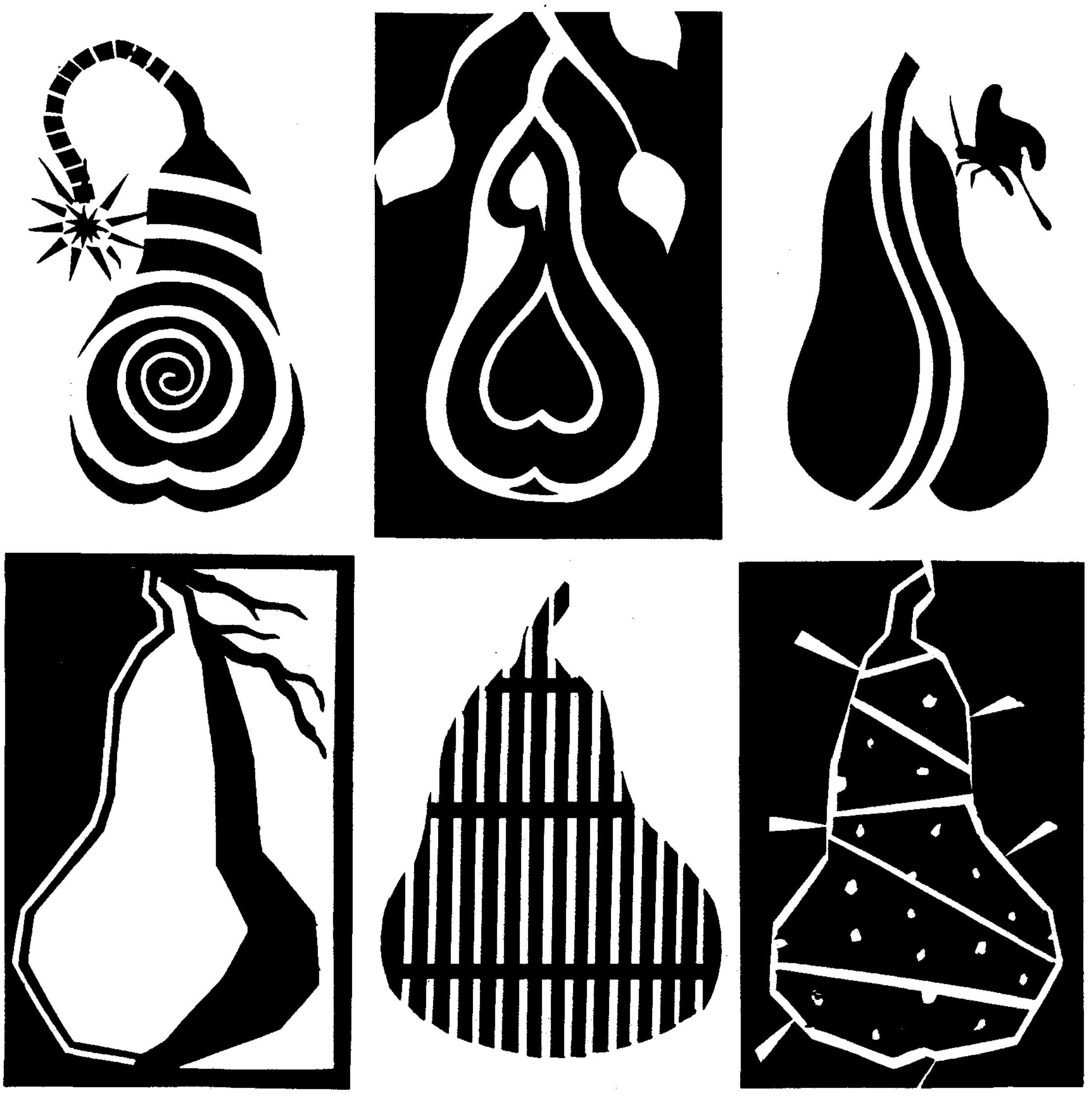


ARTHROPOD COMMUNITY ORGANIZATION AND DEVELOPMENT IN PEAR

INTRODUCTION

Arthropod communities may be composed of several hundred species populations (e.g. Oatman and Platner 1969, Wieres and Chiang 1973, Root 1973, Kogan 1981, Banerjee 1982, 1983). In evaluating the dynamics of these complex systems, researchers have recognized several important aspects of community structure, organization and development. Habitat, trophic, life history and species pool aspects have been incorporated in developing a perspective for understanding the structure, organization, and development of arthropod communities in pear (Liss et al. 1982)

Arthropod communities in pear and other crops can be understood to have a complex hierarchical organization in which levels of organization or subsystems can be recognized between the species population level and the community as a whole (Liss et al. 1982) (Fig. 1). Hierarchical classification schemes are an effective method of dealing with the dimensionality of complex systems (Allen and Starr 1983). The notion of "levels of organization" being integrated through hierarchical arrangement is an important part of many early attempts to develop general biological frameworks (Warren et al. 1979).

Arthropod community structure is taken to be an empirical concept entailing the kinds, abundance and distribution of subsystems composing the community. Community organization is a more theoretical concept. It entails the incorporation, concordance and interpenetration of community subsystems and their environments. The notion of concordance implies harmonious and perhaps rule-like relationships between subsystems. Subsystems of arthropod communities are organized through habitat, trophic and life history requirements and interactions.

The early work of Elton (1966, Elton and Miller 1954) and more recently Southwood (1977) emphasized the importance of habitat perspectives in understanding community structure and organization. A number of other studies have indicated that the richness or diversity of arthropod species inhabiting a plant is related to its structural complexity or architecture (e.g. Lawton and Schroeder 1977, Lawton 1978, 1983, Strong and Levin 1979, Moran 1980).

Liss et al. (1982) take community habitat structure and organization to be the primary basis of community structure and organization and a major determinant of community subsystems in pear. The habitat of a system is defined as a place having the capacity to provide environmental conditions suitable for the persistence of the system. The habitat can be conceptualized as being composed of a hierarchy of habitat subsystems. Habitat subsystems and conformant community subsystems in pear are shown in Figure 1.

Species interrelationships such as predation, parasitism, herbivory, competition and mutualism are important elements of the

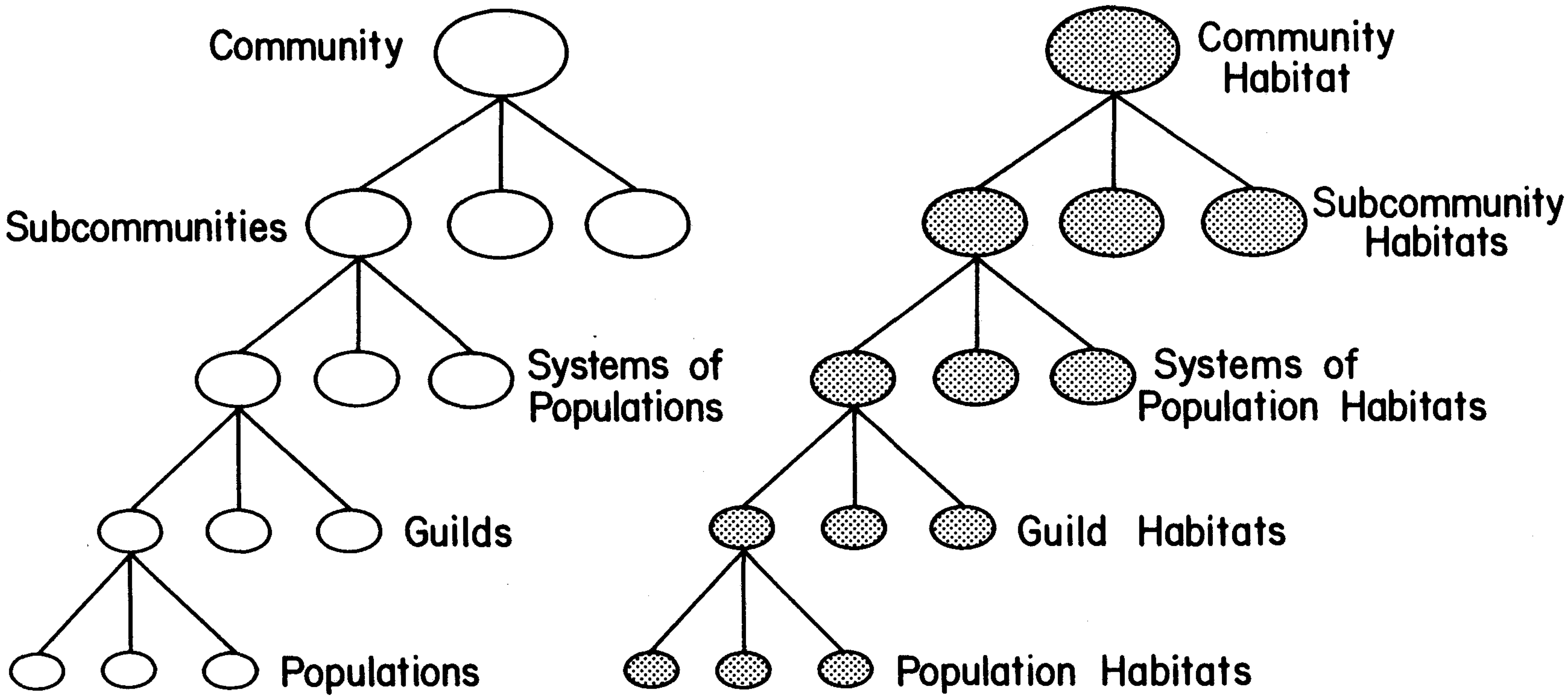


Figure 1. Possible hierarchical structure of some kinds of arthropod communities (e.g., pear) and their conformity with the structure of the community habitat.

trophic organization of communities. Functional groups and guild associations (Root 1973, Lawton 1982, Moran and Southwood) have been conceptualized based on trophic relationships and, for phytophagous species, site and mode of feeding. Trophic relationships are taken to form the basis of organization of some systems of populations and guilds in pear.

The role or importance of interspecific interactions, particularly competition, in structuring arthropod communities continues to be debated (Ratchke 1976, Connor and Simberloff 1979, Connell 1980, Lawton and Hassell 1981, Lawton and Strong 1981, Lawton 1982, Moran and Southwood 1982, McClure 1983). Most recently, some insect ecologists have argued for an individualistic view (sensu Gleason 1917, 1926), essentially maintaining that species will come to colonize a site as a result of their individual life history traits and will remain if environmental and habitat conditions are suitable (Simberloff 1978, Lawton and Strong 1981, Price 1983, 1984). As emphasized by these authors, life histories of individual species populations play an important role in organizing communities.

Community development is defined as change in structure and organization through time and is conceptualized as being jointly determined by the development of the community habitat and the organization of the species pool (Liss et al. 1982).

A number of studies have emphasized the relationship between the growth and development of an individual plant and changes in the kinds and abundance of arthropods developing on it (Price 1976, Mayse and Price 1978, Lawton 1978, 1983, Kogan 1981). More specific efforts have been directed toward understanding the relationship between seasonal changes in the chemical and physical attributes of a plant and changes in the abundance and distribution of closely associated arthropod species (see chapters in books edited by Rosenthal and Janzen, 1979, and Denno and McClure, 1983).

The species pool can be conceptualized as the system of arthropod communities that provide colonists to pear. Arthropod communities may develop differently in different species pools (Liss et al. 1982, Gut et al. in preparation). Arthropod ecologists have examined the role of the species pool in determining colonization and community development principally within the framework of MacArthur and Wilson's (1976) island biogeography model.

The work reported herein is an evaluation of the utility of the approach explicated by Liss et al. (1982) in understanding and in explaining the structure, organization, and development of arthropod communities in pear. Habitat, trophic, and life history aspects of community structure and organization are investigated. Emphasis in this study is on the role or importance of habitat development in determining arthropod community development. Seasonal development of the pear arthropod community is evaluated in relation to the development of the tree.

MATERIAL AND METHODS

Study Area

Approximately 4,000 hectares of pear are grown in the Rogue Valley near Medford, Oregon. Over the past six years, arthropod communities in pear have been investigated at several locations in this southern Oregon valley. The most extensive work has been conducted at the Hanley Station, Southern Oregon Agricultural Experiment Station, Medford, Oregon. At this site in 1982, arthropod community organization and development was studied in a 0.6 ha. block of Bartlett (Williams) pears. The orchard received no insecticide treatments from 1980-1982 and in 1978-1979 was only treated with pheromone and a minimally disruptive insect growth regulator (diflubenzuron) for control of codling moth, *Cydia pomonella*. The trees are approximately 25 years old, are commercially maintained in terms of orchard practices other than pesticide use and are moderately vigorous, i.e. 30-50 cm/year of new growth. The vegetation in this area is predominantly agricultural crops. The study orchard is bounded on two sides by small blocks of sprayed pear and other fruit orchards. A mosaic of non-insecticide treated fields of alfalfa, grain crops, grass seed, corn, sunflowers and melons extend south of the unsprayed pear orchard. To the east is a small stream and associated patches of riparian vegetation.

Evaluation of Habitat Organization and Development

Seasonally an individual pear tree, like other perennials, offers a continually changing availability of habitats for arthropods. The developing pear tree exhibits bud swelling and bloom in early spring followed shortly by full leaf expansion and woody shoot growth which continues through early summer. By mid-summer, depending upon competition with fruit for moisture, shoot growth slows or ceases but growth of fruit continues until the late summer harvest period. Harvest is followed by leaf senescence and fall leaf drop. Chemical or physiological changes associated with structural changes also occur as the pear tree develops. To date, there have been few studies concerning the relationship between these chemical and nutritional factors and the relative suitability of pear as an arthropod habitat. Initial investigations of *P. communis*, the species from which most European and American cultivars have been derived, have not as yet identified any primary or secondary plant substances that could be related to dramatic restrictions in arthropod or disease fauna or flora (Challace 1969, 1972, Challace and Westwood 1972). However, the genus *Pyrus* shows variability in the degree of resistance to *Psylla pyricola* Foerster (Westigard et al. 1970) and *Eriosoma pyricola* Bak. and David. (Westwood and Westigard 1969).

Based on this general knowledge of the developmental pattern of the pear habitat, five sample periods were selected in which to examine both habitat development and arthropod community development. Sampling began in early February and continued through late July. The five sample periods coincided with major morphological changes in habitat composition and were termed Dormant (DO), Budswell (BS), Bloom (BL), Expanded-Leaf/Small Fruit (LF) and Mature Leaf/Summer (SU). In presenting some results, dormant and budswell data have been averaged to compensate for contagious distributions early in the season and in these cases the time period has been termed early season (ES).

Each of the major above-ground habitat subsystems (i.e., wood, fruit and leaf subcommunity habitats) change morphologically during the season and over longer periods of time. Therefore it was necessary to divide these growth stages into subcategories referred to here as developmental states. The developmental states for each of the subcommunity habitats are given in Table 1.

On two trees, measurements of the distribution and abundance of each developmental state of each subcommunity habitat were made during each sampling period. Measurement of the surface area and biomass of older wood (developmental states 2-4 of the wood subcommunity) were made only once, in late summer, since seasonal changes in the abundances of these developmental states were difficult to measure. In addition, calculations of their biomass only took into account bark and associated structures.

To determine the abundance of each developmental state of the leaf subcommunity habitat, seventy leaf spurs, fruit spurs and new shoots from each tree were tagged early in the season, and the

Table 1. Description of the developmental states of arthropod subcommunity habitats in pear.

I. Developmental States of the Wood Subcommunity Habitat

State	Symbol	Description
1	W1	new green wood less than one year old
2	W2	wood with smooth uncreviced bark
3	W3	wood with roughened bark covered with moss and lichens
4	W4	old wood with fissured, creviced bark

II. Developmental States of the Fruit Subcommunity Habitat

State	Symbol	Description
1	FB	dormant fruit bud
2	FB	delayed dormant fruit bud (bud swell and loosening of bud scales)
3	BL	full bloom
4	YF	early fruit set - young small fruit
5	OF	older fruit
6	RF	tree ripe fruit

III. Developmental States of the Leaf Subcommunity Habitat

State	Symbol	Description
1	LB	dormant leaf bud
2	LB	delayed dormant leaf bud (bud swell and loosening of bud scales)
3	UL	unexpanded leaf to early expansion
4	NL	new leaf state - very young leaf, light green in color, velutinous
5	OL	old leaf state - older leaf, dark green in color, indurate
6	SL	senescent leaf state - very old leaf, yellow in color, translucent

number of leaves of each leaf developmental state present at that time were counted. This procedure was repeated on the tagged structures during each of the four remaining sample periods. In addition, on each sample date, five leaf spurs, fruit spurs, and shoots from each of several locations in the tree were removed and brought back to the laboratory where leaf surface area and biomass measurements were taken. Average values for each group of five were calculated and used to estimate the surface area and biomass of leaves on tagged structures. The number, surface area and biomass of leaves of each developmental state on each tree were determined. This entailed multiplying the average number, surface area and biomass of leaves of each developmental state per tagged leaf spur, fruit spur and shoot by the total number of these structures on the tree (determined from counts of the total number of leaf spurs, fruit spurs and shoots on each tree in late summer).

Similar procedures were used to determine the abundances of new wood (developmental state 1 of the wood subcommunity habitat) and each developmental state of the fruit subcommunity habitat. The abundance of fruit was found by multiplying the average number, surface area, and biomass of fruit per spur at each sample date by the total number of spurs per tree.

Evaluation of Arthropod Community Organization and Development

Three sampling strategies were employed to determine the arthropod species composing the community and their abundance on each developmental state of each subcommunity habitat. The most intensive method involved the removal of subcommunity habitats and determination of the kinds and abundances of species present. Prior to removing a subcommunity habitat from a tree, it was carefully examined for the presence of mobile arthropods such as generalist predators or adults of phytophagous forms. Mobile arthropods which were observed were identified, counted, and the developmental state of the subcommunity habitat where they were found was recorded. After being removed, the plant structure was examined under a dissecting microscope and the kinds and abundances of observed arthropod species were recorded. At each sample date, four samples of each developmental state were taken from each of two trees. Each of the eight major samples was comprised of leaf spurs, fruit spurs, new shoots (when present) and sections of wood developmental states 2 through 4 from a particular spatial location in the tree. Species abundances per tree were estimated by multiplying their average densities on subcommunity habitat developmental states from each location on the tree by the corresponding average number of each structure per tree.

In addition to plant part removal, four 30 minute timed observations were made at each sample date to record the abundance and feeding of the more active species.

Limb tapping also was used to determine arthropod species composing the community. This procedure entailed jarring branches with a rubber covered piece of wood dowling and recording the number and kinds of arthropod species falling onto a 46 cm x 46 cm cloth covered catching frame (Burts and Retan 1973). Single limbs on each of twelve trees were tapped during each sample period.

Though many arthropod species were recorded by all sampling methods, others were recorded only by a single method. In cases where particular arthropods were found by more than one sampling technique, data were summarized based on that sample type which was judged to reflect the most accurate measure and, in most cases, the greatest abundance of that taxa. Whenever possible, plant part removal or observation data were used, since these included information on habitat utilization patterns. Plant part removal samples were generally used for less mobile species and/or lifestages. Arthropods found in this way were often the most abundant. Direct observations were used for more mobile, but generally less abundant, taxa and lifestages. Limb taps were used to assess relative abundances of many of the generalist predators, as well as mobile adults not feeding on pear, such as small dipterans.

All unidentified arthropods, as well as a small sample of the known species were collected and preserved in 70% ethanol. Arthropod biomass estimates were obtained by drying (60^{o}C) representative samples of the various life stages of each species present during each sample period, weighing them on an electronic balance and multiplying the dry weight per individual by the total number of individuals recorded.

Trophic habits and guild classifications were based on knowledge of the biology and morphology of the arthropod species gained from the literature, as well as field observations. Following Root (1973), phytophagous arthropod guilds were determined on the basis of site and mode of feeding of phytophagous species. Other non-carnivore guilds were defined based on the habitat used by various life history stages. Predators were classified as generalists if their range of prey included members of several community subsystems and if they were also likely to move outside the orchard to feed. Information concerning the feeding relationships of parasitoids or hyperparasitoids on pear is lacking in the literature and only a few additional observations were made during this study.

Data Management and Analysis

A Scientific Information Retrieval (SIR) data management system was used to store and organize data from this study. This system allows for the generation of reports, scattergram plots of data and output files to be used for further analysis.

Discriminant analysis was used to investigate seasonal changes as to the discreteness of arthropods placed in the various subcommunity habitats. The analysis enables the researcher to statistically distinguish between two or more pre-selected groups. Groups are distinguished based on a set of discriminating variables that measure characteristics on which the groups are expected to differ. Linear combinations of the discriminating variables (discriminant functions) are formed in such a way as to maximize the separation of the groups (Pimental 1979, Klecka 1975). Leaf, fruit and wood subcommunities were distinguished based on the relative abundances of taxa-lifestage combinations present during a particular sample period.

Species richness, relative abundance and biomass measurements were used to evaluate arthropod community structure, organization and development. Utilization of subsystem biomasses is one effective means of discussing, in a general sense, the development of community subsystems above the species population level. In this way, the dynamics and possible interrelationships of these higher levels of organization can begin to be illustrated.

RESULTS

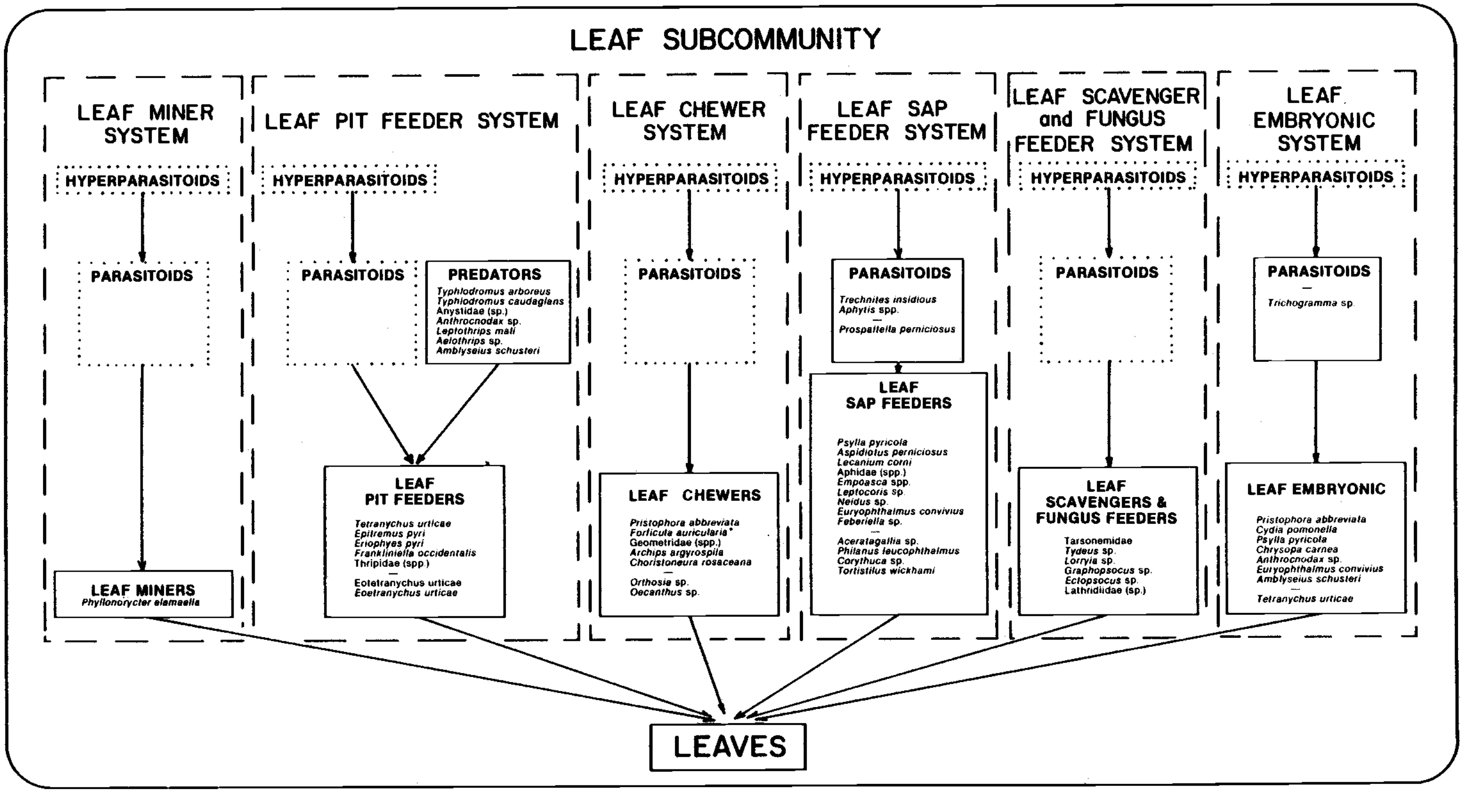
Arthropod Community Subsystems in Pear

Community habitat is taken to be the major determinant of arthropod community structure and organization in pear. Arthropod subcommunities develop on wood, fruit and leaf subcommunity habitats (Figures 2 a-c). Pear subcommunities are composed of several trophically organized systems of populations. Each system of populations is organized around a guild of arthropods that utilize the subcommunity habitat in a similar way, that is as sites for feeding, overwintering, shelter or reproduction (embryonic guild). In each system of populations, guilds of parasitoids, hyperparasitoids and predators may be associated with these other guilds.

The kinds and abundance of arthropods that comprise these community subsystems change seasonally and thus, not all taxa listed in Figures 2 a-d are present at any one time during the year. Table 2 presents information concerning seasonal changes in the kinds and abundance of species populations associated with pear at the study site (entries above the dash in each box in Figures 2 a-d). Additional taxa listed in these figures (below the dash) were not encountered at this study site but do inhabit pear at another southern Oregon location the implications of which will be discussed in a later paper.

Figure 2. Arthropod community in pear. Leaf (a), fruit (b), and wood (c) subcommunities can be recognized. Each of these subcommunities is composed of one or more trophically organized systems of populations. Each system of populations is composed of a guild of phytophagous, embryonic or overwintering arthropods and associated guilds of predators, parasitoids and hyperparasitoids. (d) The general predators take their prey from a number of systems of populations or subcommunities and help integrate the various community subsystems. Arrows indicate interactions between groups of species. Taxa listed as members of each guild are divided into those utilizing pear at Hanley in 1982 (above the dash) and those found at another southern Oregon location in 1982 (below the dash). Some taxa listed above the dash are also members of the pear arthropod community at this second location. Not all species are present at any one time.

a.



LEAF SUBCOMMUNITY
LEAF MINER SYSTEM
HYPERPARASITOIDS
PARASITOIDS
LEAF MINERS
Phyllonorycter elmaella
LEAF PIT FEEDER SYSTEM
HYPERPARASITOIDS
PARASITOIDS
PREDATORS
Typhlodromus arboreus
Typhlodromus caudaglans
Anystidae (sp.)
Anthrocnodax sp.
Leptothrips mali
Aelothrips sp.
Amblyseius schusteri
LEAF PIT FEEDERS
Tetranychus urticae
Epitremus pyri
Eriophyes pyri
Frankliniella occidentalis
Thripidae (spp.)
—
Eotetranychus urticae
Eoetranychus urticae
LEAF CHEWER SYSTEM
HYPERPARASITOIDS
PARASITOIDS
LEAF CHEWERS
Pristophora abbreviata
Forficula auricularia*
Geometridae (spp.)
Archips argyrospila
Choristoneura rosaceana
—
Orthosia sp.
Oecanthus sp.
LEAF SAP FEEDER SYSTEM
HYPERPARASITOIDS
PARASITOIDS
Trechnites insidious
Aphytis spp.
—
Prospaltella perniciosus
LEAF SAP FEEDERS
Psylla pyricola
Aspidiotus perniciosus
Lecanium corni
Aphidae (spp.)
Empoasca spp.
Leptocoris sp.
Neidus sp.
Euryophthalmus convivius
Feberiella sp.
—
Aceratagallia sp.
Philanus leucophthalmus
Corythuca sp.
Tortistilus wickhami
LEAF SCAVENGER and FUNGUS FEEDER SYSTEM
HYPERPARASITOIDS
PARASITOIDS
LEAF SCAVENGERS & FUNGUS FEEDERS
Tarsonemidae
Tydeus sp.
Lorryia sp.
Graphopsocus sp.
Ectopsocus sp.
Lathridiidae (sp.)
LEAF EMBRYONIC SYSTEM
HYPERPARASITOIDS
PARASITOIDS
—
Trichogramma sp.
LEAF EMBRYONIC
Pristophora abbreviata
Cydia pomonella
Psylla pyricola
Chrysopa carnea
Anthrocnodax sp.
Euryophthalmus convivius
Amblyseius schusteri
—
Tetranychus urticae
LEAVES

Figure 2.

b.

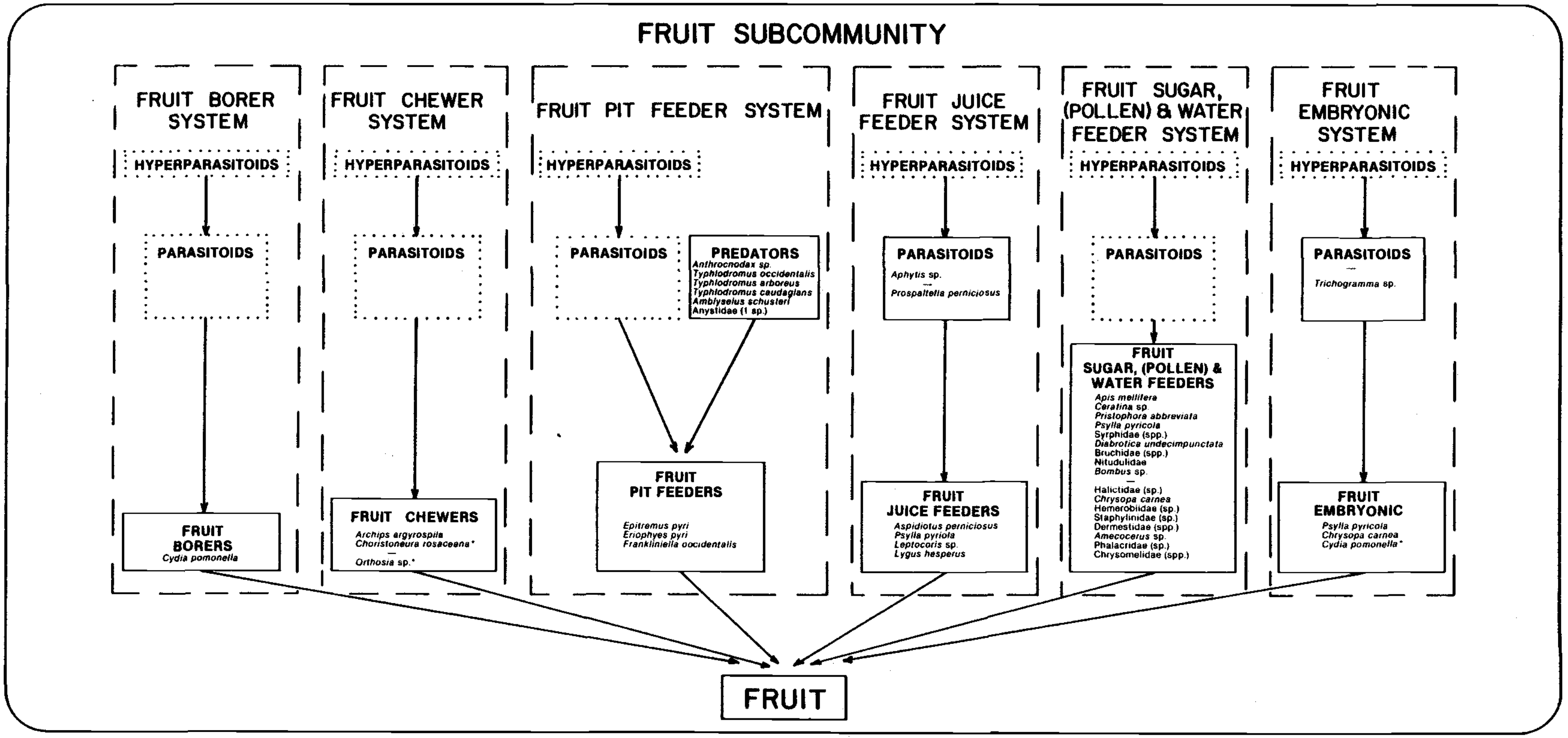


Figure 2 continued.

c.

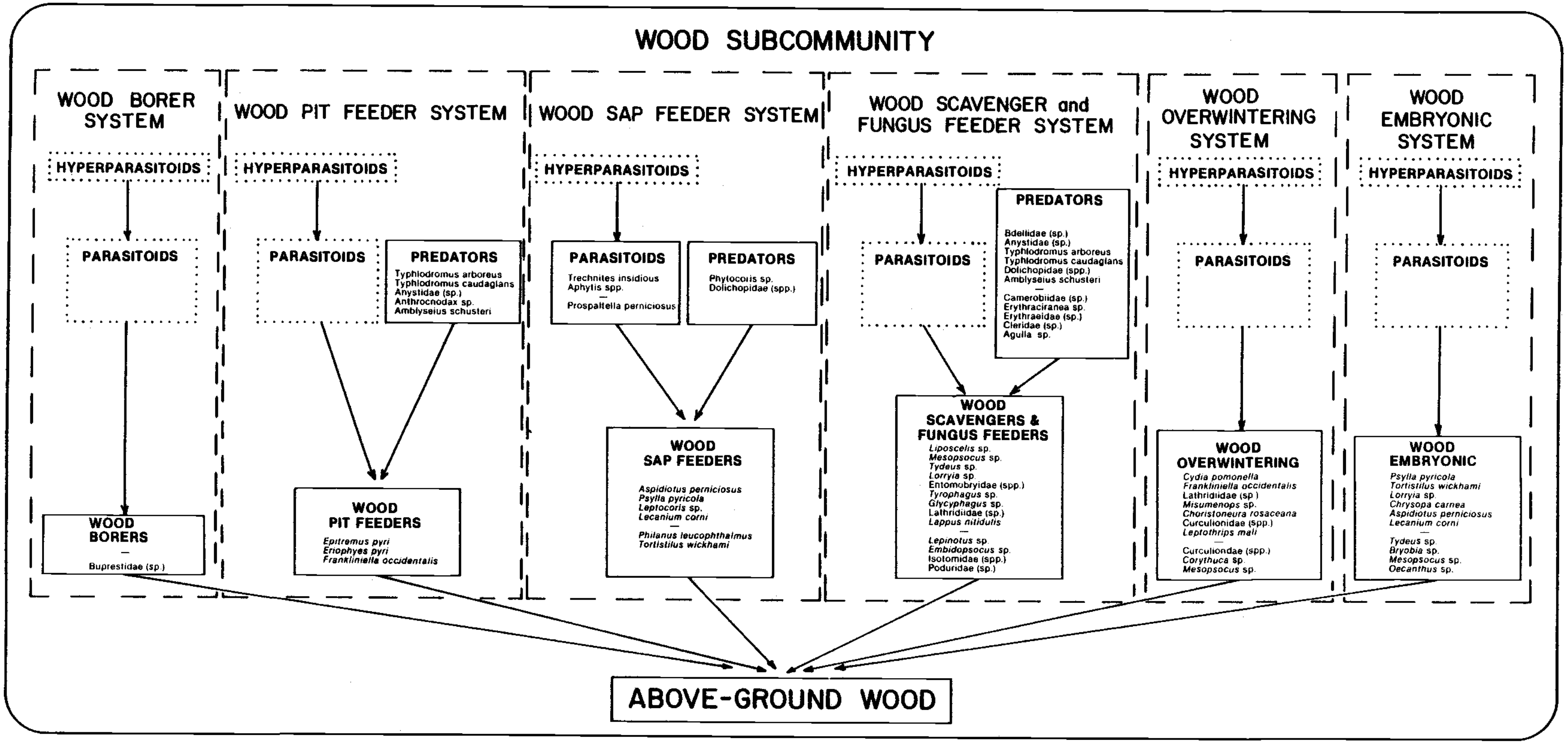


Figure 2 continued.

d.

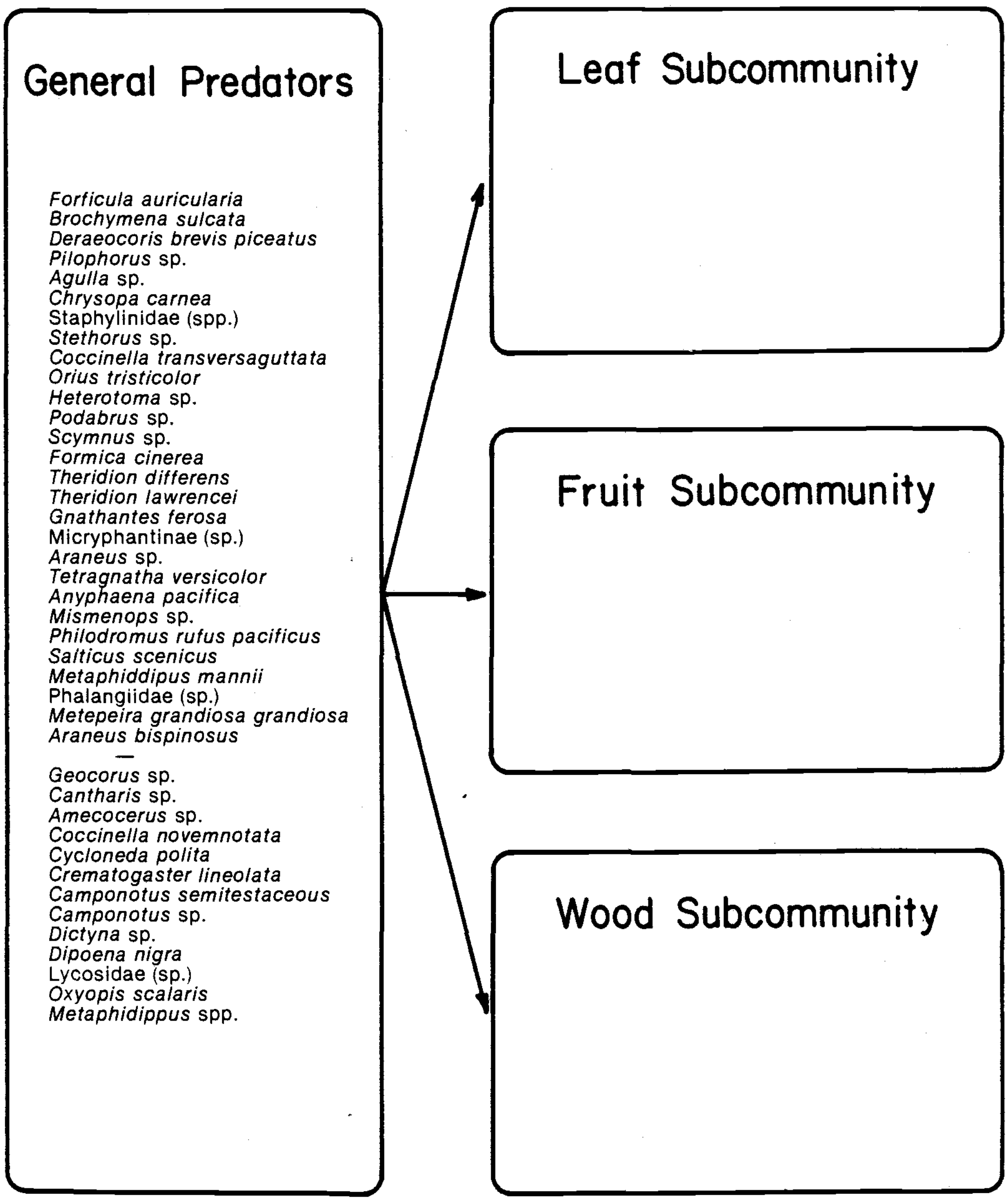


Figure 2 continued.

Table 2. List of taxa comprising each guild of arthropods found on pear at the Hanley site in 1982. Their abundances per tree, for plant part removal sampling (P), per 8 observation periods (O), or per 12 limb taps (T) are recorded for each sample period. Capital letter symbols refer to the following lifestages or subcommunity habitats: A (adult), P (pupa), C (pupa or larva in cocoon), L (larva), N (nymph), PE (post-embryonic), ES (immatures in egg sac), E (egg), W (wood), F (fruit), and L (leaf).

TAXA	LIFESTAGE	SAMPLING METHOD	EARLY SEASON SUB-C	EARLY SEASON ABUND	BLOOM SUB-C	BLOOM ABUND	EXPANDED LF SUB-C	EXPANDED LF ABUND	SUMMER SUB-C	SUMMER ABUND
HERBIVORE GUILDS										
BORERS										
Cydia pomonella (L.)	L	P					F	23	F	303
MINERS										
Phyllonorycter elmaella Dog.	L	P							L	22
PIT FEEDERS										
Tetranychus urticae (Koch)	PE	P					L	5		
Epitremus pyri (Nalepa)	PE	P	WFL	6416	WFL	27325	WFL	746005	WL	38277
Eriophyes pyri (Pgst.)	PE	P	WFL	7236	FL	1403	WFL	183250	WL	541254
Frankliniella occidentalis (Pergande)	A,L	P			F	2	FL	2844	WL	609
Thripidae - Adult 1	A	O,T			F	2	-	31		
Adult 2	A	P					L	54	L	117
CHEWERS (STRIP FEEDERS)										
Pristophora abbreviata (Hartig)	L	P			L	262	L	536		
Diabrotica undecimpunctata (Mann.)	A	O							L	3
Geometridae - Larva 1	L	O					L	1		
Larva 2	T	T					-	1		
Archips argyrospila (Walker)	L	O			F	1	L	4		
Choristoneura rosaceana Harris	L	O,P					L	2	L	12
SAP OR JUICE FEEDERS										
Neidus sp.	A	O							L	2
Empoasca sp.	A	T							-	2
Feberiella sp.	A	O							L	1
Leptocoris sp.	A,N	O			WFL	4	WL	2		
Euryophthalmus convivius (Stal)	A	O					L	1		
Lygaeidae - Adult 1	A	O							L	1
Lygus hesperus Knight	A	O			F	1				
Aphidae - Post-embryonic 1	PE	P							L	77
Post-embryonic 3	PE	T							-	1
Post-embryonic 4	PE	T							-	3
Post-embryonic 5	PE	O					L	4		
Post-embryonic 7	PE	T							-	2
Post-embryonic 8	PE	T			-	1				
Aspidiotus perniciosus (Comstock)	A,N	P	WF	4468	WL	4719	W	2861	WFL	12035
Lecanium corni (Bouche)	A,N	P	W	486	W	340	W	174	L	9769
Psylla pyricola Foerster	A,N	P,O			WFL	1551	WL	5629	L	303
SCAVENGERS AND FUNGUS FEEDERS										
Tyrophagus sp.	PE	P	W	5						
Glycyphagus sp.	PE	P	W	91						
Tydeus sp.	PE	P	W	141	W	39	WL	106	WL	643
Lorryia sp.	PE	P	W	600	W	1406	W	414	W	2093
Tarsonemidae - Post-embryonic 1	PE	P					L	82	L	18
Lappus niditulis (Lec.)	A	P					W	11	W	12
Lathridiidae - Adult 1	A	T							-	6
Ectopsocus sp.	A	T							-	1
Ectopsocidae - Adult 1	A	T							-	1
Graphopsocus sp.	A	T							-	2
Liposcelis sp.	A,N	P	W	110	W	62				
Mesopsocus sp.	A,N	P					W	72		
Entomobryidae - Post-embryonic 1	PE	O	W	1						
Post-embryonic 2	PE	P,T	W	15					-	1
Post-embryonic 3	PE	T	-	1						
SUGAR(POLLEN) AND WATER FEEDERS										
Syrphidae - Adult 1	A	O			FL	3				
Adult 3	A	O			F	1				
Adult 5	A	O			F	1				
Diabrotica undecimpunctata (Mann.)	A	O			F	1				
Nitidulidae - Adult 1	A	O			FL	11				
Bruchidae - Adult 2	A	T			-	1				
Apis mellifera (L.)	A	O			F	25				
Bombus sp.	A	O			F	1				
Ceratina sp.	A	O			F	1				
Pristophora abbreviata (Hartig)	A	O,T			FL	8.				
Psylla pyricola Foerster	A	T			-	5				
Chrysopa carnea Stephens	A	T			-	1				
OVERWINTERING										
Misumenops sp.	ES	O	W	12						
Metaphidippus mannii (G. & E. Peckham)	ES	O	W	6						
Curculionidae - Adult 1	A	P	W	55						
Adult 2	A	O	W	1						
Lathridiidae - Adult 1	A	P	W	7						
Psylla pyricola Foerster	A	O	W	9						
Micro-hymenoptera - Adult 1	A	P	W	20						
Cydia pomonella (L.)	C	P	W	13	W	9			W	9
Choristoneura rosaceana Harris	C	P	W	10						
Frankliniella occidentalis (Perg.)	A	P	W	17						
Thripidae - Adult 1	A	P	W	6						
Leptothrips mali (Fitch)	A	P	W	58					W	555
EMBRYONIC										
Pristophora abbreviata (Hartig)	E	P			FL	1607	L	83		
Cydia pomonella (L.)	E	P					L	88		
Liposcelis sp.	E	P			W	68				
Leptocoris sp.	E	P,O			W	9	W	1		

Table 2.

TAXA	LIFESTAGE	SAMPLING METHOD	EARLY SEASON SUB-C	EARLY SEASON ABUND	BLOOM SUB-C	BLOOM ABUND	EXPANDED LF SUB-C	EXPANDED LF ABUND	SUMMER SUB-C	SUMMER ABUND
Euryophthalmus convivius (Stal)	E	P					L	77		
Psylla pyricola Foerster	E	P	WL	885	WFL	3582	WFL	11761	L	782
Tortistilus wickhami (VanDuzee)	E	P	W	41					W	3
Amblyseius schusteri Chant	E	P					L	32	L	11
Lorryia sp.	E	P			W	1085				
Anthrocnodax sp.	E	P					WL	21		
Syrphidae - Egg 1	E	P					L	8		
Chrysopa carnea Stephens	E	P					FL	126	L	47
CARNIVORE GUILDS										
PIT FEEDER PREDATORS										
Typhlodromus arboreus (Chant)	PE	P	W	15	FL	71	L	10	WL	56
Typhlodromus caudaglans Schuster	PE	P					L	6		
Amblyseius schusteri Chant	PE	P					WFL	52	WL	141
Anystidae - Post-embryonic 1	PE	P,T					L	17	-	1
Anthrocnodax sp.	L	P					L	18		
Aelothrips sp.	A	T							-	1
Leptothrips mali (Fitch)	A	P,T			W	20	WL	81	-	1
STRIP FEEDER PARASITOIDS										
Parasitized *Archips argyrospila*	PE	O							L	1
SAP FEEDER PREDATORS										
Dolichopidae - Adult 1	A	O	W	1			W	1	W	12
Adult 2	A	T					-	2		
Phytocoris sp.	A,N	P			W	11	WL	238	WL	146
SAP FEEDER PARASITOIDS										
Trechnites insidiousus (Crawford)	PE	P					W	25		
Aphytis spp.	PE	O,T			W	2	-	2	W	2
SCAVENGER AND FUNGUS FEEDER PREDATORS										
Typhlodromus arboreus (Chant)	PE	P	W	38	W	71	WL	20	WL	68
Typhlodromus caudaglans Schuster	PE	P					L	6		
Amblyseius schusteri Chant	PE	P	W	35	W	30	WFL	74	WL	163
Bdellidae - Post-embryonic 1	PE	P	W	25						
Anystidae - Post-embryonic 1	PE	P,O					L	17	-	1
Dolichopidae - Adult 1	A	O	W	1			W	1	W	12
Adult 2	A	T					-	2		
GENERAL PREDATORS										
Theridion differens Emerton	A,N	O	L	1	WFL	4	WL	4	L	9
Theridion lawrencei (G. & A.)	A	T							-	3
Gnathantes ferosa (Chamberlin & Ivie)	A,N	T					-	2	-	4
Eriogonidae (Micryphantinae) - Species 1	A,N	O,T			F	1	-	4	-	3
Metepeira grandiosa grandiosa (C. & I.)	A	T							-	1
Araneus bispinosus (Keys.)	A	O					W	1		
Araneus sp.	A	T	-	1						
Tetragnatha cfr. *versicolor* Walckenaer	A	T							-	1
Anyphaena pacifica (Banks)	A	O							L	1
Misumenops sp.	A,N	T			-	4	-	2		
Philodromus rufus pacificus Banks	A,N	T			-	1	-	1		
Salticus scenicus (Clerck)	A	O							W	1
Metaphidippus mannii (G. & E. Peckham)	A,N	O,T	L	1			-	1	L	30
Phalangiidae - Species 1	A,N	O					W	1	WL	2
Forficula auricularia L.	A,N	T							-	6
Brochymena sulcata VanDuzee	A	T,O					-	1	L	1
Orius tristicolor (White)	A	T							-	1
Deraeocoris brevis piceatus Knight	A,N	T					-	2	-	10
Heterotoma sp.	A.	T							-	1
Pilophorus sp.	A	T							-	1
Agulla sp.	A	O					L	1		
Chrysopa carnea Stephens	L	T							-	10
Staphylinidae - Adult 1	A	O					L	1		
Adult 3	A	T					-	1		
Podabrus sp.	A	O					WFL	7		
Stethorus sp.	A	T			-	1	-	1		
Scymnus sp.	A	T					-	1	-	1
Coccinella transversaguttata Fald.	A	O							L	1
Empididae - Adult 1	A	O					L	1		
Syrphidae - Larva 1	L	O							L	1
Vespidae - Adult 1	A	O							L	1
Formica cinerea Mayr	A	P					W	1		
NOT PLACED IN GUILDS										
Ceratopogonidae - Adults 6,7,9	A	T			-	4	-	1	-	4
Chironomidae - Adults 1,2,7,8,10,11,12,14,18	A	T	-	3	-	13	-	20	-	9
Cecidomyiidae - Adults 4,8	A	T			-	1			-	3
Drosophilidae - Adult 3	A	T			-	1	-	1		
Chloropidae - Adults 1,4,5,7	A	T			-	4	-	4	-	3
Sciaridae - Adult 1	A	T							-	1
Tachinidae - Adult 1	A	T			-	1				
Syrphidae - Adults 2,3	A	O					L	2		
Psychodidae - Adults 1,2	A	T							-	2
Bruchidae - Adult 1	A	T,O					-	2	L	1
Halictidae - Adult 1	A	O					L	1		
Pristophora abbreviata (Hartig)	A	T					-	1		
Caliroa cerasi (L.)	A	O					L	1		
Psyllidae - Adult 1	A	O					L	1		
Phyllonorycter elmaella Dog.	A	T					-	1		
Chrysopa carnea Stephens	A	O,T					L	2	-	4
Hemerobiidae - Adult 1	A	O							L	1

Table 2 continued.

Most systems of populations in pear can be organized around a guild of phytophagous arthropods. Phytophagous guilds are comprised of arthropod taxa that have a similar site and mode of feeding. In the structuring of guilds on pear, I have followed the terminology of Root (1973).

Pit Feeders - Pit feeders rasp the substrate and feed on exuding cell contents. Pit feeding guilds exist on wood, fruit and leaves. Eriophyid mites, *Epitremus pyri* (Nalepa) and *Eriophyes pyri* (Pgst.), are the most abundant members of this guild in all three subcommunity habitats (Table 2). Additional pit feeders include species of thrips, primarily *Frankliniella occidentalis* (Pergande), and tetranychid mites such as *Tetrarychus urticae* (Koch). Pit feeding on the wood subcommunity habitat is restricted to current year's woody growth (developmental state W1).

Sap (Juice) Feeders - Sap or juice feeders probe into the plant and feed on juices. Wood, fruit and leaf associated guilds are present. Members of these guilds include all of the phytophagous hemipterans. San Jose scale, *Aspidiotus perniciosus* (Comstock), and pear psylla, *Psylla pyricola* Foerster, are the most abundant species in all three subcommunity habitats (Table 2), while brown apricot scale, *Lecanium corni* (Bouche), is also prevalent in the wood and leaf sap feeding guilds. Within the wood subcommunity, pear psylla only feeds on new green (W1) wood, while both species of scale may utilize older wood developmental states (W2-W4) as well.

Chewers (Strip Feeders) - Chewers or strip feeders chew pear fruit or foliage. Members of the fruit chewing guild include some lepidopteran larvae such as the fruit tree leafroller, *Archips argyrospila* (Walker). Leafroller and other lepidopteran larvae are also members of the leaf chewing guild. However, the most abundant leaf chewer in this study was the larva of pear sawfly, *Pristophora abbreviata* (Hartig).

Sugar (Pollen) and Water Feeders - Sugar and water feeders utilize flower nectar and pollen or sugar solutions and water that accumulate on the fruit surface. Members of this guild include several species of Hymenoptera, primarily *Apis mellifera* (L.), flower feeding Coleoptera, syrphids, and adults of species whose immature stages are included as members of other guilds such as *Pristophora abbreviata* and *Psylla pyricola*.

Wood Borers - Wood borers were found feeding inside developmental state 2 wood. Although this guild was not present at the Hanley site, larvae of a single species of buprestid beetle have been found at other locations in southern Oregon.

Fruit Borers - Fruit borers penetrate the fruit surface and feed on the inner pulp. In southern Oregon, the guild is restricted to a single, important pest species, *Cydia pomonella* (L.).

Leaf Miners - Leaf miners feed on the parenchymous tissue located between the upper and lower leaf surface. Again, the guild is represented in southern Oregon by a single species, *Phyllonorycter elmaella* Dog.

Non-carnivorous arthropods may utilize pear in ways other than for feeding on wood, fruit or leaf tissue. In light of this, an additional six guilds were recognized.

Scavengers and Fungus Feeders - Scavengers and fungus feeders feed on detritus that accumulates on the wood or leaf surface and/or on wood associated fungi. This is a loosely interpreted group of arthropods whose trophic position was primarily ascertained from the literature (Borror et al. 1976, Krantz 1978, Richards and Davies 1977). Abundant taxa in the wood scavenger and fungus feeding guild include glycyphagid and tydeid mites, as well as psocids in the genera *Liposcelis* and *Mesopsocus*. Early instar tydeids, as well as a tarsonemid mite are abundant on leaves.

Embryonic - Species that deposit eggs on or in pear wood, fruit or leaves are members of this guild. Designation of this kind of guild was prompted by the recognition that some species may utilize a particular subcommunity habitat as adults or larva but deposit eggs on other parts of the pear tree. In addition, insertion of eggs into the plant tissue by some species, such as the buffalo treehopper, *Tortistilus wickhami* (Van Duzee) may have an important impact on the habitat. In the case of the buffalo treehopper, hatching larvae soon drop to the ground to feed on herbaceous plants and there is little feeding by adults or immatures on the pear tree (Yothers 1934). Commonly encountered eggs at the Hanley site include those of *Cydia pomonella*, *Pristophora abbreviata*, *Psylla pyricola*, *Chrysopa cornea* Stephens, and several of the mite taxa.

Overwintering - Overwintering species are those which either continue their life histories on or colonize and inhabit the pear tree during the fall and winter. The guild is primarily comprised of arthropods that overwinter in the older developmental states of the wood subcommunity habitat. Abundant members include *Cydia pomonella* and *Choristoneura rosaceana* Harris larvae or pupae in cocoons, as well as adults of several Coleoptera and the thrips *Frankliniella occidentalis* and *Leptothrips mali* (Fitch).

Carnivore Guilds - Recognition of carnivore guilds is based on the relative host specialization of parasitoids, hyperparasitoids and some predators. Little is known about the parasitoids and hyperparasitoids that feed on pear associated arthropods in southern Oregon. Observations of parasitism during the course of this study focused on the few species of parasitoids for which background information was available. These included *Trechnites insidiosus* (Crawford), a pear psylla parasitoid, *Prospaltella perniciosus* Tower and *Aphytis* spp., scale parasitoids, and *Trichogramma* sp., a codling moth egg parasitoid. Predator guilds are associated with wood scavengers and fungus feeders, wood sap feeders, and wood, fruit and leaf pit feeders. A complex of mites feeds on wood scavengers and fungus feeders. Wood sap feeders, primarily scale insects, appear to be among the favored prey of *Phytocoris* spp. adults and nymphs. A more varied complex of predators is associated with the pit feeding guild. In addition to the phytoseiids, *Tyhplodromus arboreus* (Chant), *T. caudaglans* Schuster, *Amblyseius schusteri*

Chant, and other predaceous mites, a cecidomyid larva, Anthrocnodax sp., and a predaceous thrips, Leptothrips mali (Fitch) are abundant predators of pit feeders.

General Predators - General predators may take their prey from a number of community subsystems. In this way they serve as arthropod community "integrators" (Root 1973), and help couple or bind together subcommunities and/or other community subsystems (Figure 2d). The importance of these generalist predators as biological control agents in pear in southern Oregon and in other regions is well documented (Madsen et al. 1963, McMullen 1964, Westigard 1979, Gut et al. 1982, Burts 1983). Abundant members of this group include several species of spiders (e.g. Theridion differens Emerton, Gnathantes ferosa (Chamberlin and Ivie), Metaphidippus mannii (G. and E. Peckham) and Misumenops sp.), Chrysopa carnea larvae, Podabrus sp. adults, Deraeocoris brevis piceatus Knight adults and nymphs and Forficula auricularia L (placed in carnivore guild based on Carroll and Hoyt, 1984).

Habitat Development

An individual tree is taken to be the habitat of the pear arthropod community. As the tree grows or develops seasonally and over longer periods, its structure and organization changes. Plant growth entails addition or loss of subcommunity habitats and development of existing subcommunity habitats (Table 1). Seasonal habitat development of pruned pear trees at the Hanley site is illustrated in Figure 3. Early in the season (average of dormant

Figure 3. Seasonal development of an individual pear tree. Along the X axis , habitat structure during each of the four sample periods is represented by a cluster of three bars. From left to right, the bars in each cluster refer to habitat biomasses in the wood, fruit and leaf subcommunities. Symbols for habitat developmental states (subsections of each bar) are defined in Table 1.

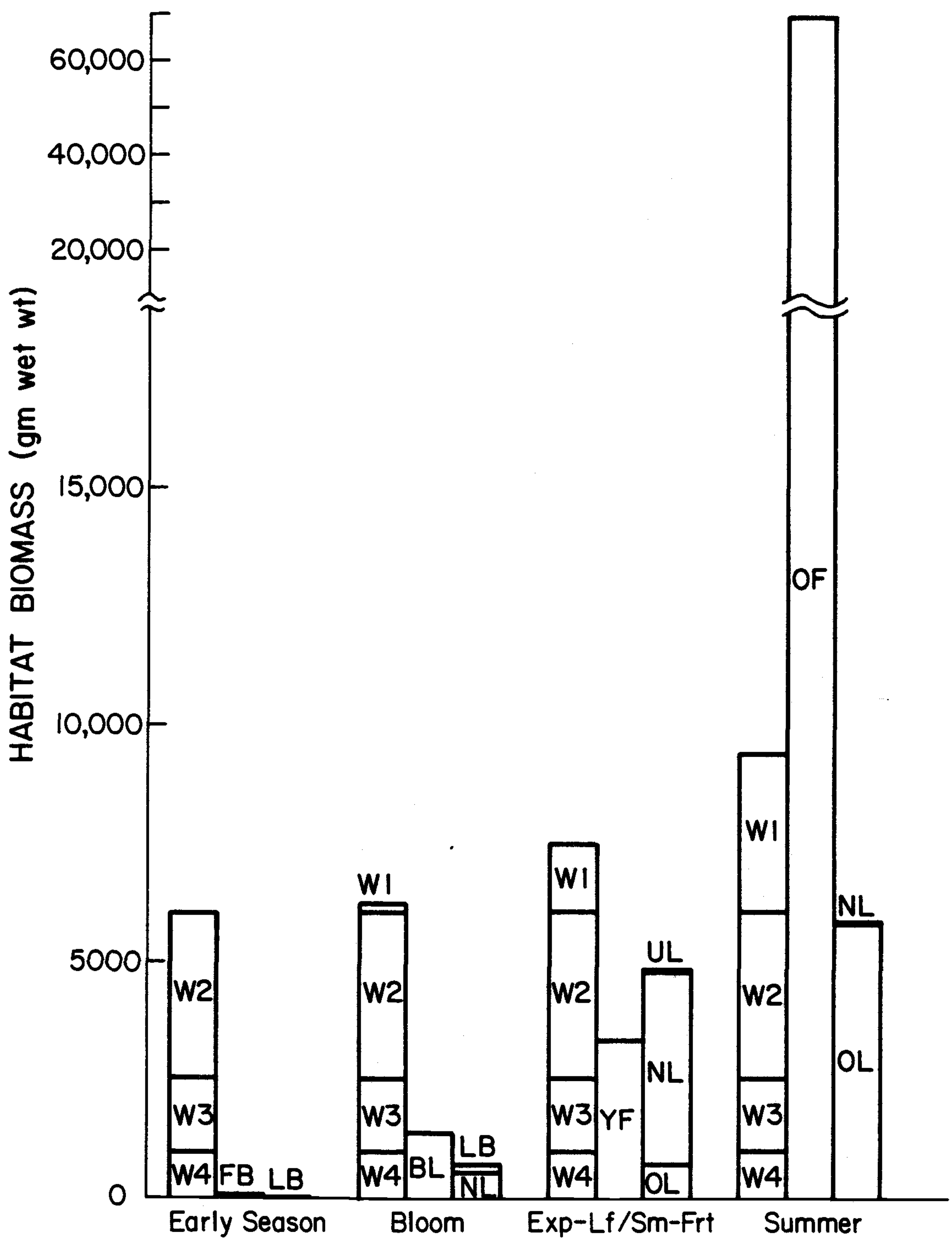

HABITAT BIOMASS (gm wet wt)
60,000
40,000
20,000
15,000
10,000
5000
0
W1
W2
W3
W4
FB
LB
BL
NL
YF
UL
OL
OF
Early Season
Bloom
Exp-Lf/Sm-Frt
Summer

Figure 3,

and budswell measurements), habitat biomass is concentrated in the wood subcommunity. Three longer-term developmental states of this subcommunity habitat are present. W2 wood comprises the largest proportion of wood habitat with over twice as much biomass as the older wood developmental states (W3, W4) combined. As discussed in the methods section, only the bark and associated substrate were included in determining the weight of both older states.

At bloom, fruit and leaf biomasses increase and new green wood (W1) is added. At this time the leaf subcommuity habitat is composed of unexpanded leaf buds (LB) and new leaves associated with fruit clusters (NL).

Leaf spur and shoot expansion occur in the early spring (expanded leaf/small fruit stage). Shoot expansion results in an increase in new green wood (W1), and the addition of a large number of associated new leaves. Older, indurate, primary fruit spur leaves (OL) and new leaves associated with expanded leaf clusters are also present. At this time the fruit subcommunity habitat is comprised of young pears (YF). Fruit develop quickly and constitute the largest portion of the community habitat in the summer. In addition, by summer new green wood comprises a large portion of the wood subcommunity habitat. Few new leaves are present in the summer.

Arthropod Community Development

Changes in the structure and organization of the arthropods community are associated with changes in plant structure and organization. Figure 4 illustrates seasonal changes in the discreteness of arthropod subcommunities in pear. Group centroids summarize the wood, fruit and leaf group locations in the (reduced) space defined by the discriminant functions. Early in the season (dormant), separation of the wood subcommunity by the first function is highly significant and accounts for 97.5% of the variation between the groups. At this time leaf and fruit subcommunities are not distinguishable. Only a few arthropods, primarily eriophyid mites, utilize these two habitats. In addition, leaf and fruit buds probably provide similar resources. During bloom, the wood subcommunity remains highly distinguishable and leaf and fruit subcommunities are still similar. However, the fruit subcommunity is distinct in the sense that it is utilized by a number of habitat specializing flower sugar (pollen) and water feeders (Table 2). However, these taxa were primarily encountered during observations rather than in the plant part removal samples which were used to calculate the discriminant functions. Following leaf expansion, the leaf subcommunity is significantly discriminated by the first function ($r = 0.99$). In addition, the second function, which accounts for the remaining variation between groups, provides good separation of the wood and fruit subcommunities. The three subcommunities maintain their discreteness in the summer. However,

Figure 4. Plots of discriminant scores illustrating seasonal changes in the discreteness of arthropod subcommunities in pear. Numbers represent cases for leaf (1), fruit (2), and wood (3) groups. Closed circles indicate the three group centroids. Data from plant part removal samples were used in the analyses.

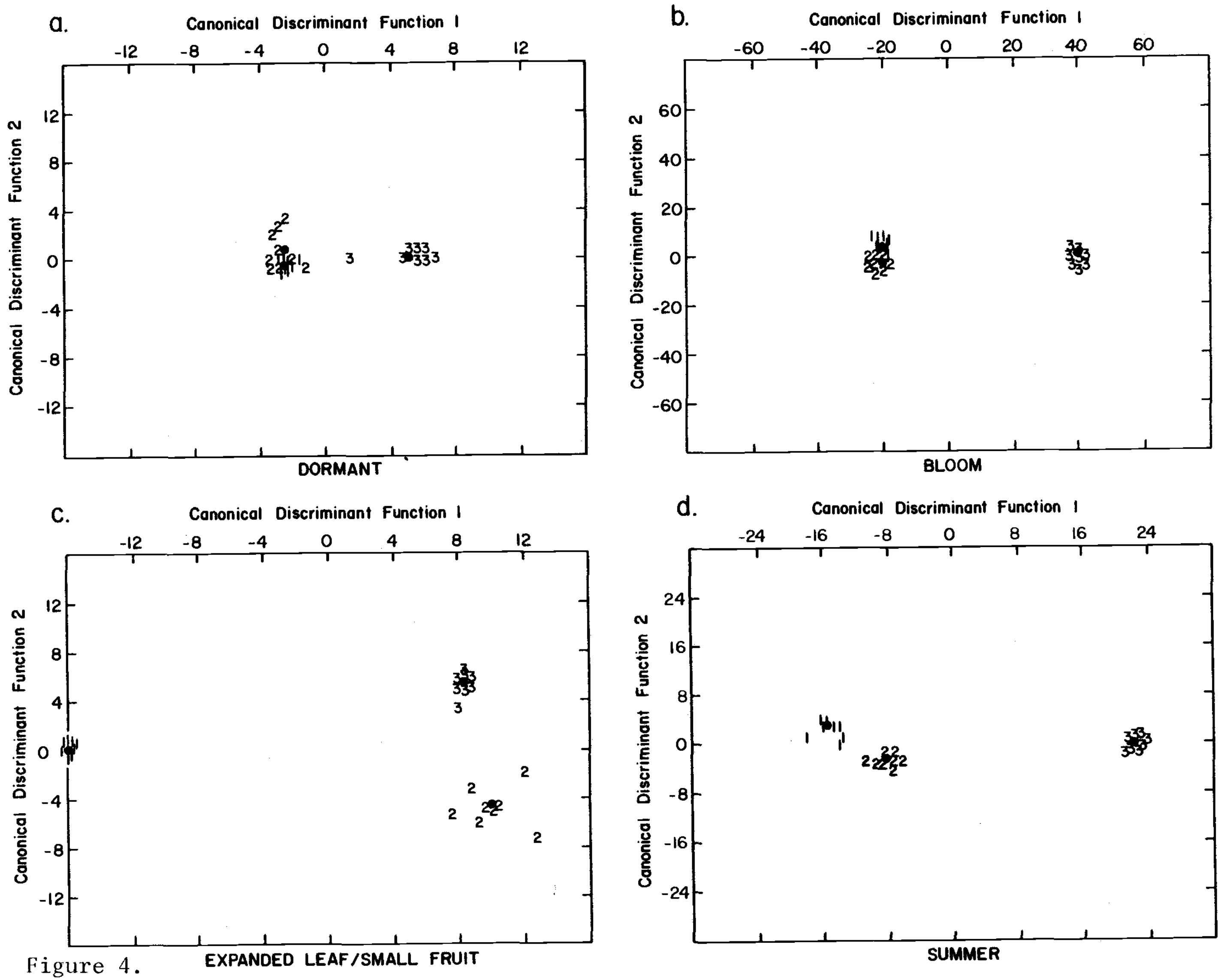

a.
Canonical Discriminant Function I
Canonical Discriminant Function 2
DORMANT
b.
Canonical Discriminant Function I
Canonical Discriminant Function 2
BLOOM
c.
Canonical Discriminant Function I
Canonical Discriminant Function 2
EXPANDED LEAF/SMALL FRUIT
d.
Canonical Discriminant Function I
Canonical Discriminant Function 2
SUMMER

Figure 4.

at this time some overwintering taxa have begun to return to the wood subcommunity habitat leading to the prominence of these variables in the first function and the greater separation of this subcommunity from the other two. Only two species occupy the fruit subcommunity at this time, and one of these also feeds on leaves and new green wood, resulting in less vertical separation of the leaf and fruit subcommunities by the second function.

Development of arthropod subcommunities and their component non-carnivore guilds includes changes in their size (expressed as arthropod biomass) and in the spatial arrangement or distribution of arthropods in the various developmental states of each subcommunity habitat (Figure 5). The number of taxa associated with each guild throughout the season is shown at the top of each bar. Information presented in Figure 5, in conjunction with data on species abundances listed in Table 2, provide a foundation for examining seasonal development of arthropod communities in pear.

Early in the season nine non-carnivore guilds are present. Five are in the wood subcommunity, two in the leaf subcommunity and two in the fruit subcommunity (Figures 5a-c). Arthropod biomass is concentrated in the wood subcommunity which also makes up the greatest biomass of habitat. Within this subcommunity, the sap feeding and overwintering guilds are dominant. Sap feeding scale and overwintering codling moth are the most abundant taxa in terms of biomass. More particularly, scale are most abundant on wood developmental state 2, while codling moth and other overwintering

Figure 5. Seasonal development of pear (a) wood, (b) fruit, and (c) leaf arthropod subcommunities. The kinds, size and species richness (in italics above each bar) of guilds comprising each subcommunity during four sample periods is shown. Both plant part removal (solid line bars) and observation (broken line bars) data are presented. For each guild, the distribution of arthropods into the various habitat developmental states is represented by stacked bars and/or symbols as defined in Table 1. Developmental states of the fruit subcommunity are not shown, since, only a single state is present during each sample period (see Figure 3). Capital letter symbols for guilds are defined as follows: (BO) Borers, (MI) Miners, (PF) Pit Feeders, (CH) Chewers, (SF) Sap Feeders, (JF) Juice Feeders, (SC) Scavengers and Fungus Feeders, (SW) Sugar (Pollen) and Water Feeders, (OW) Overwintering, and (EM) Embryonic.

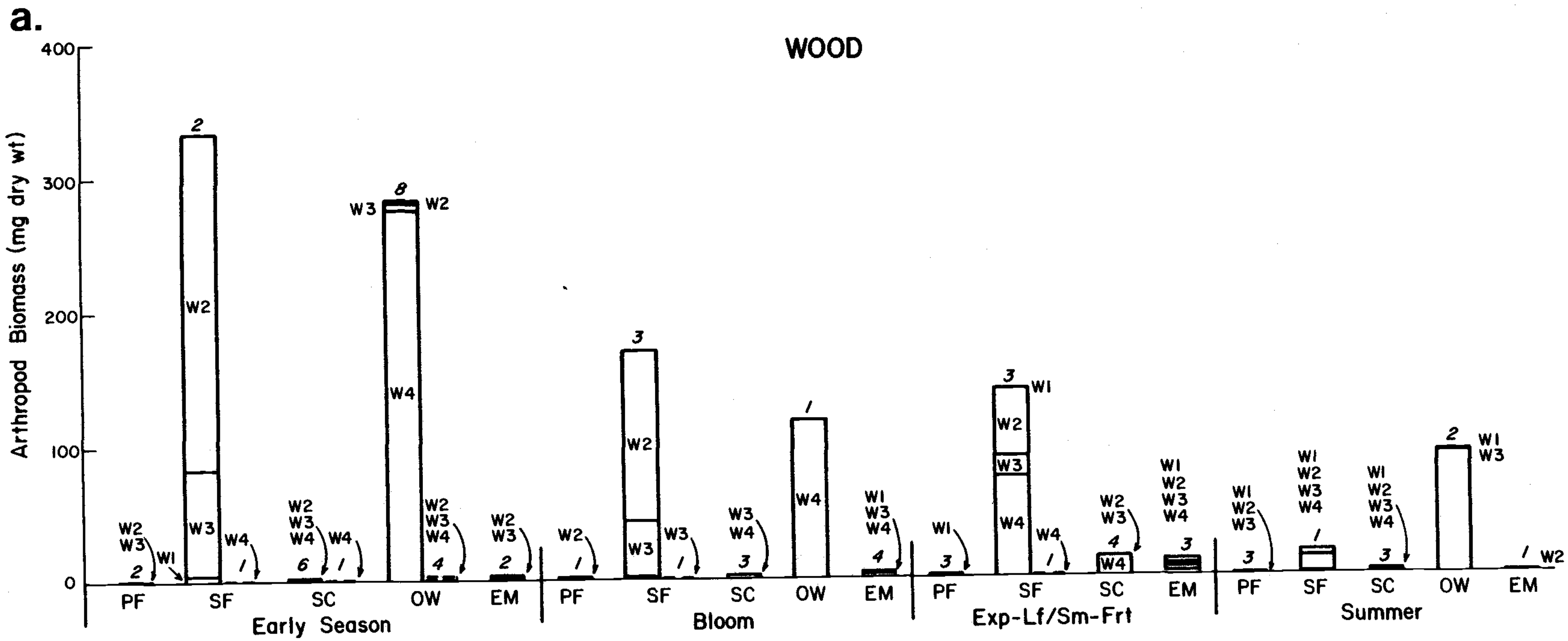

a.
WOOD
Arthropod Biomass (mg dry wt)
400
300
200
100
0
W2
W3
W4
W1
PF
SF
SC
OW
EM
Early Season
Bloom
Exp-Lf/Sm-Frt
Summer

Figure 5.

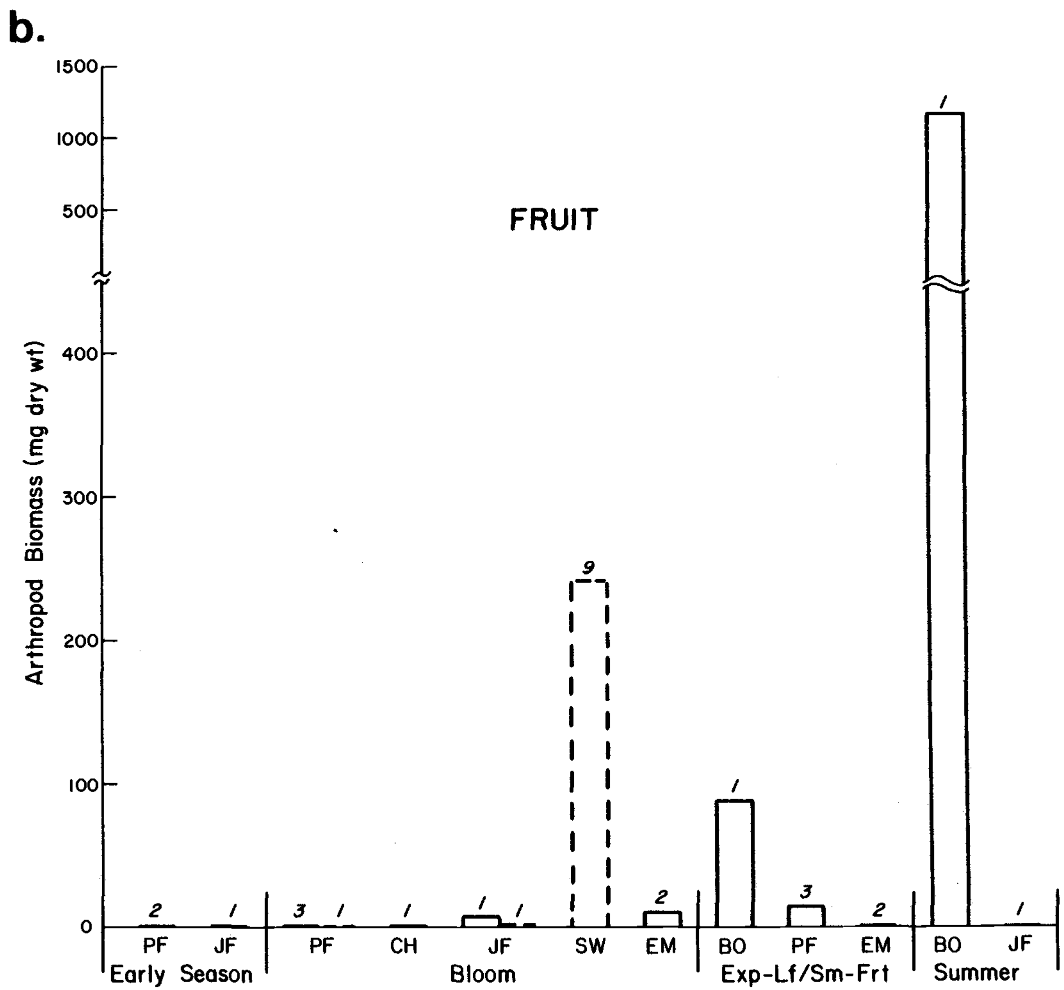


Figure 5 continued.

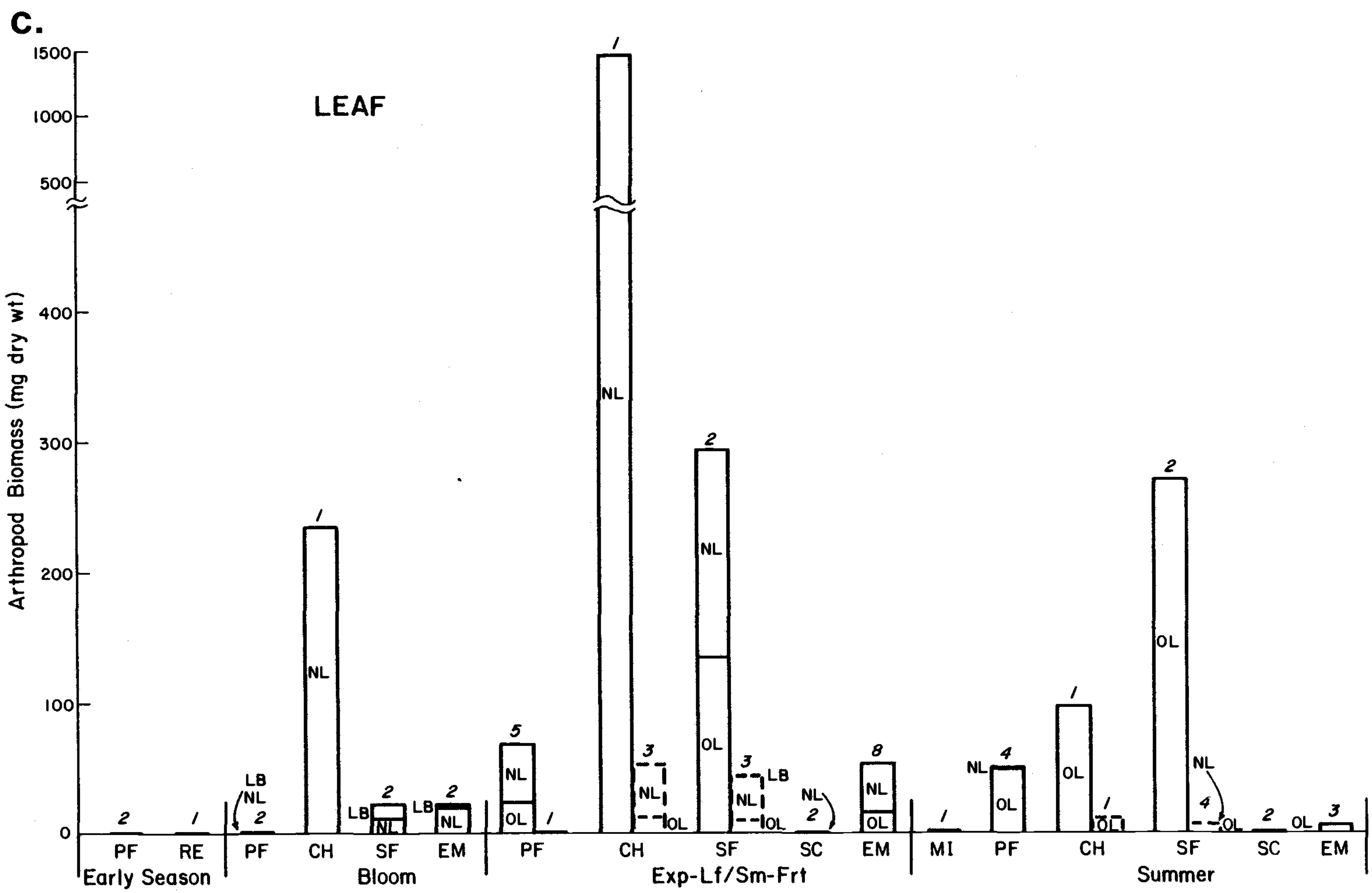


Figure 5 continued.

fauna primarily utilize wood developmental state 4. Two species of eriophyid mites (wood, fruit and leaf pit feeders) are the most abundant taxa at this time and throughout the season (Table 2), but because of their small size are not well represented in terms of biomass. A number of wood scavengers and fungus feeders are also abundant, but again, because of their small size comprise only a small portion of the total arthropod biomass.

At bloom the number of non-carnivore guilds increases to fourteen (Figures 5a-c). As fruit buds open and expand, pear flowers and new cluster leaves (Figure 3) are available for colonization by arthropods. Wood overwintering taxa begin to emerge, with some species moving to the fruit and leaf subcommunities to feed and continue their development. Thus the size of the wood subcommunity declines. Additional increases in biomasses of the fruit and leaf subcommunities occur as species colonize from surrounding vegetation. Major guilds in these subcommunities are the fruit sugar and water feeders and the leaf chewers. A number of taxa, 9 in this study, feed on flower products. Apis mellifera (L), as well as adults of Syrphidae, Nitidulidae and Pristophora abbreviata are the most abundant members of this guild. Initiation of the leaf chewer guild results from the early colonization and subsequent development of a single species, Pristophora abbreviata, which overwinters in the soil directly below the tree. Emerging adults lay their eggs on pear and developing larvae consume nearby foliage. Flowers and new leaves provide habitat for a number of other guilds, most notably leaf sap feeders, fruit juice feeders, and leaf and fruit embryonic. Sap feeding scale are still abundant on W3 and W2 wood, and some Cydia pomonella larvae have yet to emerge from their overwintering sites on W4 wood.

Associated with the addition of new, succulent leaf spur and shoot foliage at the expanded leaf/small fruit sample period (Figure 3) is a significant increase in the biomass and abundance of arthropods comprising the leaf subcommunity. Development of this subcommunity includes major increases in the size of the leaf chewer, sap feeder and pit feeder guilds. Larvae of three lepidopteran species including the leafrollers Choristoneura rosaceana and Archips argyrospila (Walker), join Pristophora abbreviata in the leaf chewing guild and all four taxa concentrate their feeding on new foliage. Pit feeder and sap feeder biomasses are more evenly distributed between new and old leaves. Pear psylla, Psylla pyricola, nymphs are the most abundant sap feeders, while two species of eriophyid mites, Epitremus pyri (Nalepa) and Eriophryes pyri (Pgst.), and the western flower thrips, Frankliniella occidentalis (Pergarde) are the most abundant pit feeders. Although the biomass of leaf chewers is much greater than either pit feeders or sap feeders, the latter two comprise many more individuals (Table 2). This is important from the standpoint of pest management, because even though pit and sap feeders are smaller and consume less foliage, indirect damage to the fruit such as honeydew marking caused by pear psylla may occur at high abundances.

During this same sample period, the abundant leaf subcommunity habitat also is important to many species which lay their eggs on the pear tree and continue their development either on leaves, fruit or wood, e.g. Cydia pomonella, Psylla pyricola, Chrysopa carnea and a number of other predators.

Development of the fruit subcommunity at this time entails the loss of flowers and the associated sugar and water feeding guild. Pollinated flowers mature and the young developing fruit provide habitat for the fruit boring guild. Since the loss in biomass of sugar and water feeders is greater than the gain in biomass provided by colonizing fruit borers, the size of the fruit subcommunity as a whole declines. However, as mentioned for the leaf subcommunity, fruit pit feeders, though low in biomass, are abundant (Table 2) and may have their greatest impact on the pear cropping system by cosmetically damaging fruit (i.e. russetting of fruit).

Total arthropod biomass of the wood subcommunity also declines at the expanded leaf/small fruit stage. Life history as opposed to habitat aspects of organization appear to be the primary contributors to this reduction. They include the loss of the overwintering guild and the decline in biomass of sap feeders associated with maturation of scale insects, including the emergence of males.

By late summer, arthropod biomass is concentrated in the fruit subcommunity. Developing fruit comprise the greatest portion of habitat (Figure 3) and are heavily attacked by fruit boring Cydia pomonella larvae. Associated with the development of the leaf subcommunity habitat, which includes the maturation of leaves (i.e. predominance of older leaves; see Figure 3) is a reduction in arthropod biomass of the leaf subcommunity. Several species, especially those with a single generation per year, disperse to their overwintering habitats. For example, arthropod biomass of the leaf chewer guild declines as single generation pear sawfly and lepidopteran larvae conclude their feeding for the year. At this time, the leaf chewer guild is represented by a single species of leafroller, Choristoneura rosaceana, whose numbers increase in the summer with the development of second generation larvae. Other guilds such as sap and pit feeders show little if any decline in size. Crawlers of both species of scale, as well as several other sap feeders that colonize from nearby senescing vegetation feed on older leaves. Pit feeding eriophyid mites also maintain large populations on older leaves. However, Epitremus pyri numbers decline dramatically while those of Eriophyes pyri increase (Table 2). Maintenance of large numbers of eriophyid mites through the summer may have an important impact on other community members. They are an important food source for predators that may preferentially feed on other members of the pit feeding guild (Hoyt 1969). The abundance of pit feeders may decrease the production of new green wood (W1) and may also reduce photosynthesis or stress the tree in other ways (Westigard et al. 1965). This not only influences the leaf and wood habitat and potential subcommunity members during the current year, but could also reduce the size of subcommunity habitats the following year. This could include reductions in the amount of W2 wood (last year's W1 wood) and the number of fruit, i.e. size of the fruit subcommunity habitat. The leaf mining guild, composed of Phyllonorycter elmaella Dog. larvae, appears during the summer.

Development of the wood subcommunity proceeds with the reappearance of an overwintering guild as taxa which spend the winter on the tree begin to recolonize. However, the biomasses of other guilds are low despite the presence of abundant wood habitat including a large addition of new green wood. These habitats were not well utilized during the expanded leaf period. Apparently, few species at the Hanley site have life histories that are well adapted to feeding on wood at this time. However, soon after the summer sample period, scale crawlers will move to the wood and the distribution of biomasses will look more like that seen during the early season sample.

These results make it clear that there are habitat, trophic, and life history aspects involved in seasonal changes in arthropod community structure and organization. A potentially important aspect of trophic organization not yet discussed is the feeding relationships of carnivores and their prey. A number of generalist predators are abundant in the pear community (Table 2; Figures 2 and 6). In pear and in other crops this complex of carnivores plays a major role in maintaining low numbers of many phytophagous

Figure 6. Seasonal development of the generalist predator complex in pear. Both plant part removal (solid line bars) and observation (broken line bars) data are presented. Species richness is indicated in italics above each bar.

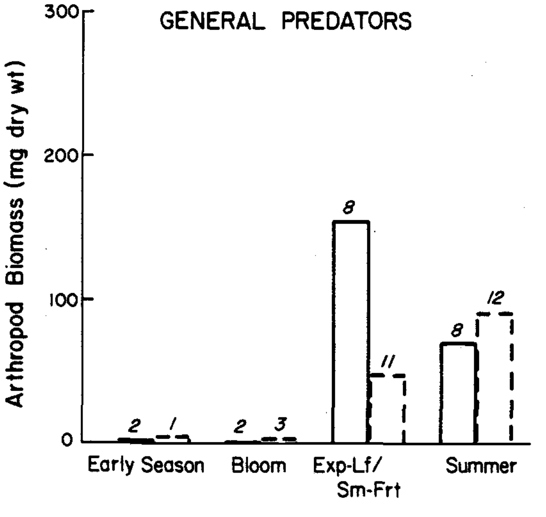

GENERAL PREDATORS
Arthropod Biomass (mg dry wt)
300
200
100
0
2
1
2
3
8
11
8
12
Early Season
Bloom
Exp-Lf/
Sm-Frt
Summer

Figure 6.

arthropods (Ehler et al. 1973, Messenger et al. 1976, Gut et al. 1982). Only a few taxa are present during the early season and bloom sample periods (Figure 6). Spiders are most abundant and probably feed on small adult dipterans. Early in the spring, at the expanded leaf/small fruit stage, spiders are still abundant but other generalist predators have colonized from overwintering sites. The kinds of insect species that colonize early varies depending on surrounding vegetation (Gut et al. 1982), but in this study the most prevalent (greatest biomass) early predator is a cantharid beetle, Podabrus sp. Adults emerge from soil or debris beneath pear trees and other locations, colonize, and feed on a number of herbivores found on the tree. Earlier work (Gut et al. 1982) has related the occurrence of similar early spring complexes of general predators to a decline in the abundance of populations of pear psylla.

Generalist predators remain relatively abundant through the summer (Table 2, Figure 6). Both the kinds and numbers of spiders increase. Predaceous insects show the same pattern with the development of populations of Deraeocoris brevis piceatus, Chrysopa carnea and Forficula auricularia. The development of this summer complex of predators was also important in maintaining low numbers of pear psylla (Gut et al. 1982).

Little information is available on parasitoids in pear in southern Oregon. Thus, placement of the more specialized carnivores into guilds depends on my own observations and information in the literature regarding these predators and parasitoids. Wood sap feeding predators are present in the greatest biomass. This guild is dominated by a predaceous mirid, Phytocoris sp., which feeds primarily on wood inhabiting scale and pear psylla. There are also complexes of predators associated with pit feeders on each subcommunity habitat as well as wood scavengers and fungus feeders. Several of these species are predaceous mites which feed on wood scavenging or fungus feeding mites early in the season but move to leaves and fruit later in the year and feed on pit feeding mites. Few parasitoids were recorded during this study, although some species that were encountered are known to occur in large numbers in southern Oregon and have an important influence on the abundances of certain pest species. Prospaltella perniciosi Tower was found in 1970 to have attacked over 80% of the San Jose scale on untreated Bartlett pear trees (Westigard 1979). Codling moth egg mortality averaging 26% has been attributed to the activity of predators and parasites including Trichogramma spp. (Westigard et al. 1975). The parasitoid Trichnites insiodiosus (Crawford) is a potentially important natural enemy of pear psylla.

Few studies have examined relationships between the seasonal development of the habitat and changes in the kinds and size of community subsystems, such as guilds. More frequently, seasonal changes in species richness or species diversity have been related to some measure of habitat diversity or complexity (Price 1975, Lawton 1978, 1983). In pear and in other communities, as the season progresses and the complexity of the habitat increases, the number of species utilizing it increases (Figure 7).

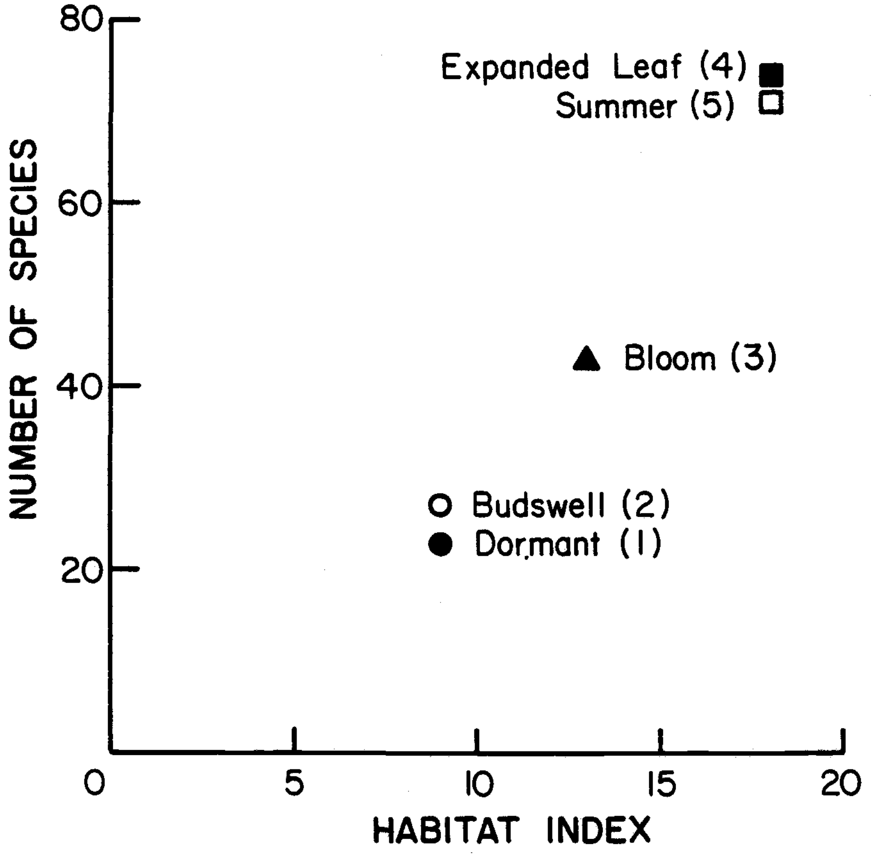


Figure 7. Relationship between the seasonal development of the pear tree (habitat index) and the number of associated arthropod species. Developmental states of each subcommunity habitat were scored from 1 to 4 depending on their relative size (biomass). Habitat index is equal to the sum of these scores for each sample period. Plant part removal, observation, and limb tap data were used in determining the number of species.

DISCUSSION

Habitat Aspects of Organization and Development

One approach to ordering or simplifying complex arthropod communities is to conceptualize them as being hierarchically organized. The organization of the habitat is considered to be the primary determinant of community organization in pear. In arthropod community ecology, habitat boundaries are often taken to define community boundaries. The arthropods inhabiting plants of diverse species in a defined area may be understood as a "compound" community, while those utilizing an individual plant species or a few plant species in a more restricted area are termed a "component" community (Root 1973). In either case, boundaries of the community habitat determine community boundaries.

Just as individual plants can be considered as component habitats of more encompassing systems, individual plant parts can be conceptualized as habitat subsystems. In pear, arthropod subcommunities develop on leaf, fruit and above-ground wood subcommunity habitats. In each subcommunity, phytophagous as well as overwintering and embryonic guilds are recognized based on the more particular ways in which subcommunity habitats are utilized.

Habitat perspectives have been useful in understanding arthropod species diversity. In the broadest sense, the structural complexity of plant types has been related to the number of species they support, trees supporting more species than woody shrubs, and these more than herbs (Lawton and Schroeder 1977, Lawton 1978, Strong and Levin 1979). More particular relationships between various measures of habitat complexity or diversity and arthropod species diversity have been demonstrated for several plant taxa and are extensively reviewed by Lawton (1983). For example, Moran (1980) showed that the number of arthropods associated with species of Opuntia cactus was related to the complexity of habitat structure. Those species with the most complex architecture supported the greatest number of insect species.

Recognition of community subsystems based on habitat aspects of structure and organization provides a basis for Waloff's (1968) discussion of the arthropod community in Scotch broom. Subcommunity habitats on broom can be taken to be seed pods, foliage and young stems, and main stems and branches (Figure 8a-c). Subcommunities are comprised of one or more phytophagous guilds, with each being determined based on site and mode of feeding. For example, in the pod subcommunity there is a guild of phytophagous arthropods that are seed feeders, another a guild of pod cavity feeders, and still another a guild of pod gall feeders.

As a pear tree or Scotch broom bush grows or develops, its structure and organization changes. Seasonal development of the pear tree includes changes in the kinds and abundance of developmental states of each subcommunity habitat. At a particular time, the habitat can be conceptualized as a spatial mosaic of

Figure 8. Arthropod community in Scotch broom. Three subcommunities can be identified; the pod subcommunity (a), the foliage and young stem subcommunity (b), and the main stem and branch subcommunity (c). Each of these subcommunities is composed of one or more systems of populations. Each system of populations is composed of a phytophagous guild, and associated guilds of predators, parasitoids and hyperparasitoids. (d) The general predators take their prey from a number of systems of populations or subcommunities and thus help integrate the various community subsystems. Arrows indicate interactions between groups of species. Not all species are present at any one time. Adapted from Waloff (1968).

a.

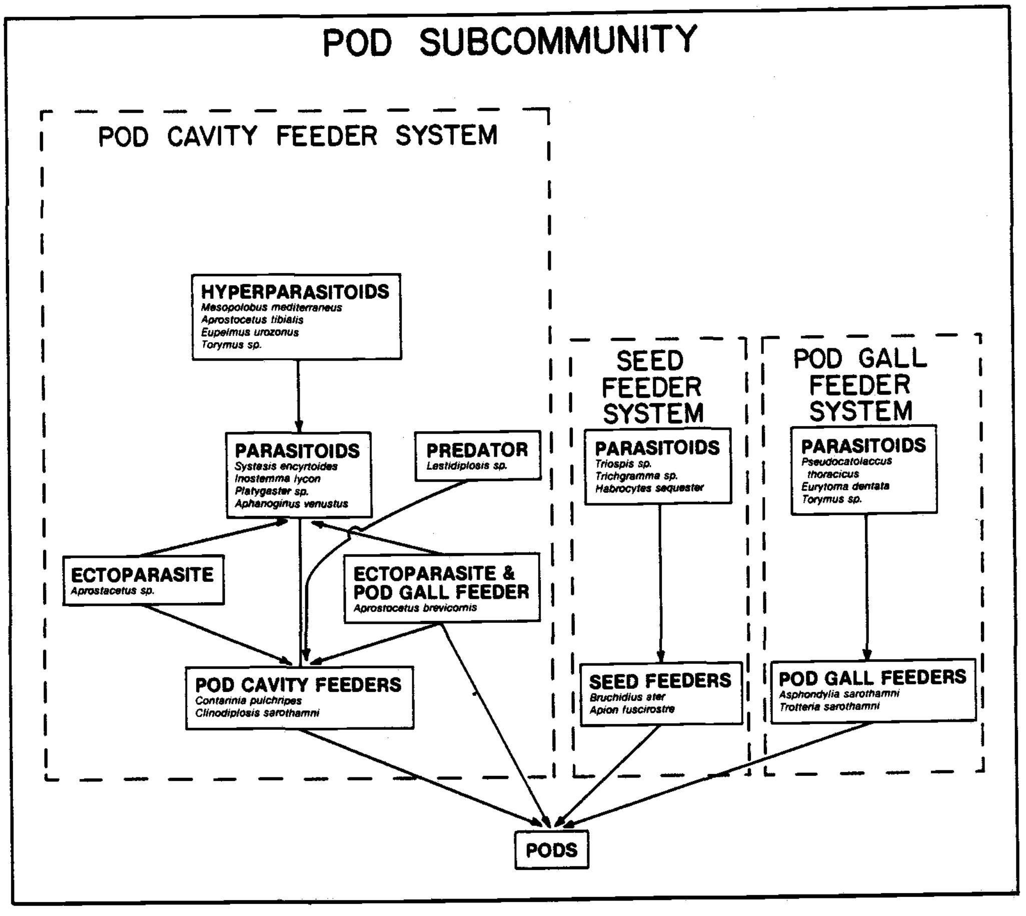

POD SUBCOMMUNITY
POD CAVITY FEEDER SYSTEM
HYPERPARASITOIDS
Mesopolobus mediterraneus
Aprostocetus tibialis
Eupelmus urozonus
Torymus sp.
PARASITOIDS
Systasis encyrtoides
Inostemma lycon
Platygaster sp.
Aphanoginus venustus
PREDATOR
Lestidiplosis sp.
ECTOPARASITE
Aprostacetus sp.
ECTOPARASITE &
POD GALL FEEDER
Aprostocetus brevicornis
POD CAVITY FEEDERS
Contarinia pulchripes
Clinodiplosis sarothamni
SEED
FEEDER
SYSTEM
PARASITOIDS
Triospis sp.
Trichgramma sp.
Habrocytes sequester
SEED FEEDERS
Bruchidius ater
Apion fuscirostre
POD GALL
FEEDER
SYSTEM
PARASITOIDS
Pseudocatolaccus
thoracicus
Eurytoma dentata
Torymus sp.
POD GALL FEEDERS
Asphondylia sarothamni
Trotteria sarothamni
PODS

Figure 8.

b.

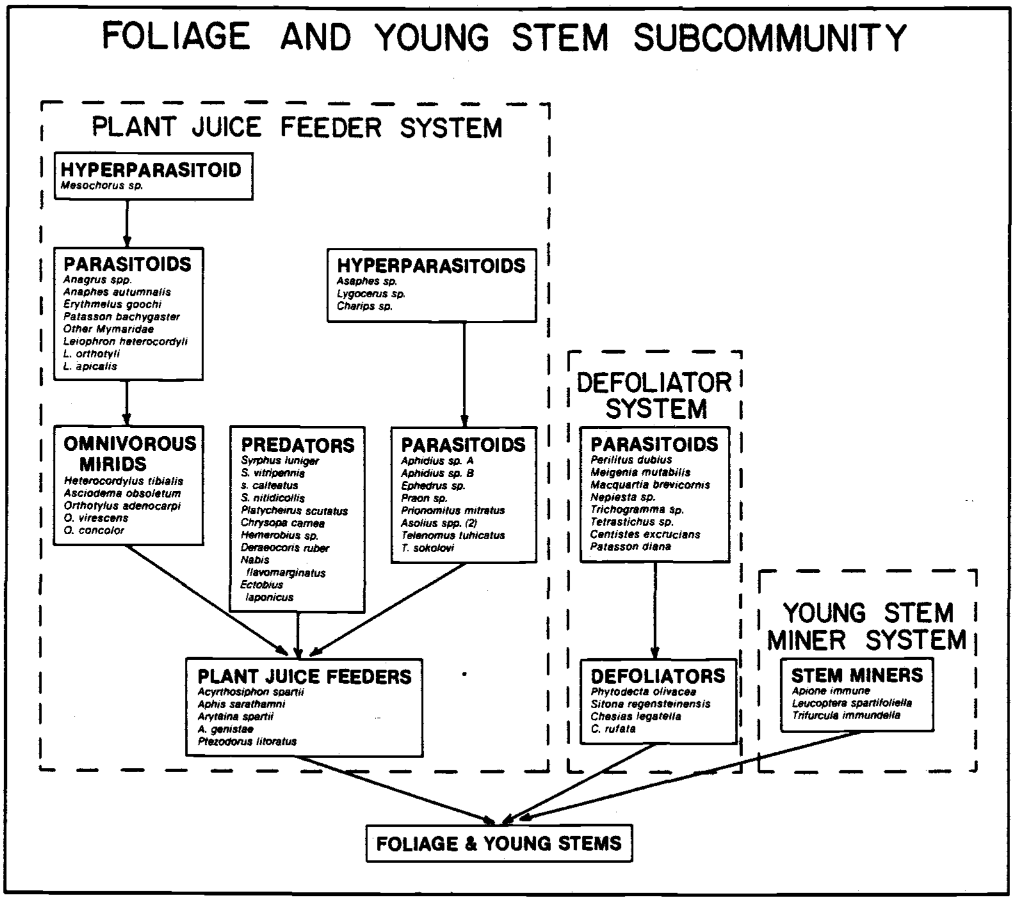


Figure 8 continued.

C.

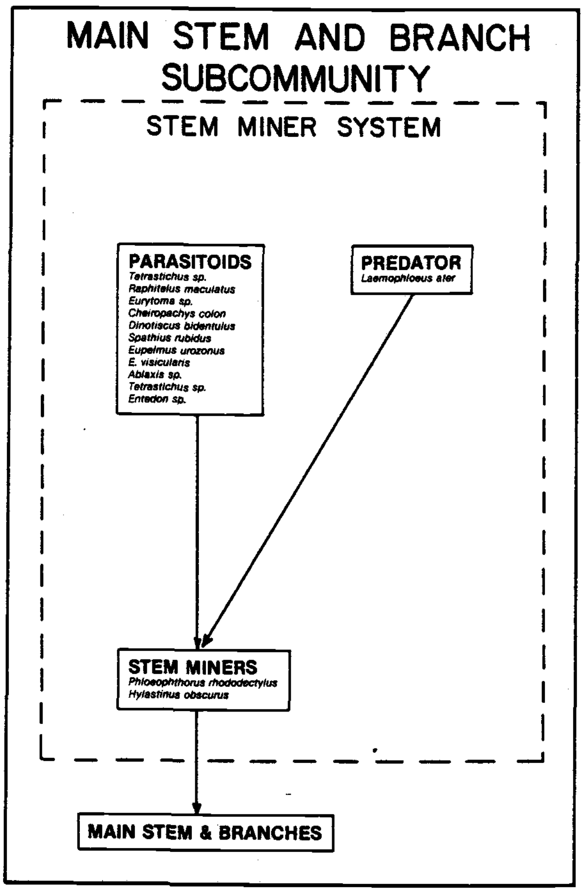


Figure 8 continued.

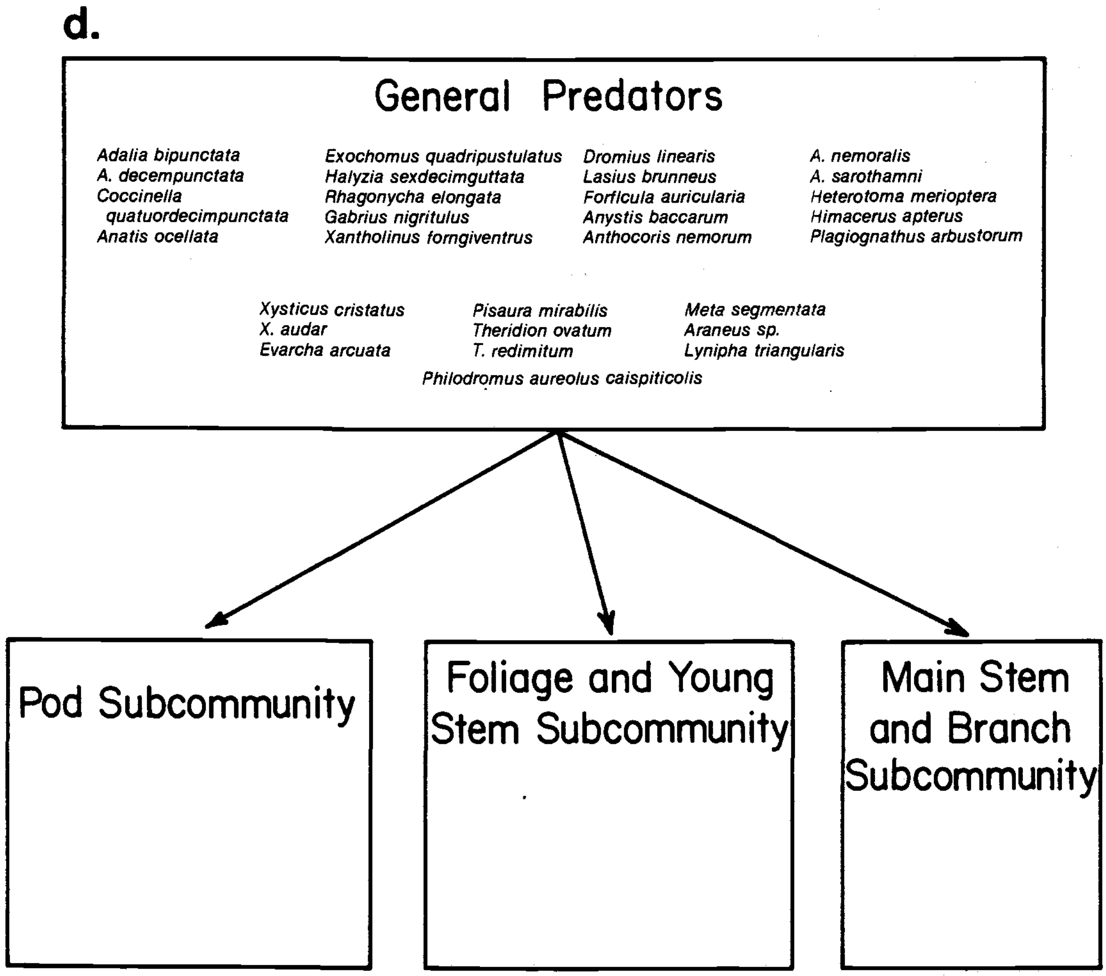


Figure 8 continued.

different habitat subsystems in different developmental states. The number of species inhabiting pear increases in relation to increases in the number and relative size of habitat developmental states.

Relationships between seasonal habitat development and the number of associated arthropod species have been investigated in bracken fern (Lawton 1978) and soybean (Price 1976, Mayse and Price). In both cases, patterns of change in species number were shown to parallel seasonal increases in habitat size. Like pear, bracken fern and soybean habitat development can be taken to entail changes in the kinds, abundance and distribution of habitat subsystem developmental states. Soybean development includes changes in the kinds, number and spatial arrangement of plant parts, as well as qualitative changes in these food resources as leaves grow older, stems grow thicker and tougher, and reproductive parts mature (Kogan 1981). It appears that seasonal changes in species composition in soybean and fern are, in part, determined by these kinds of changes in habitat structure and organization (Lawton 1978, Price 1976, Mayse and Price 1978, Kogan 1981).

In pear, development of leaf and fruit subcommunities and associated guilds also can be related to seasonal changes in habitat structure and organization. The appearance of particular guilds often parallels the appearance of guild habitats. For example, the addition of leaf chewers, fruit sugar and water feeders and fruit borers is concordant with the appearance of new leaves, flowers, and young fruit, respectively. Developing guilds also are influenced by the relative amount of habitat present and the length of time it is available. Thus, from bloom through leaf expansion, the leaf chewing guild increases in biomass in accordance with the continuing addition of new leaves. As the leaves age, leaf chewer abundance declines, while sap and pit feeding guilds continue to develop on the more available older leaves.

Seasonal development of the wood subcommunity appears to be largely determined by the individual life histories of the associated fauna. Following bloom, there is a decline in the size of wood subcommunity as several arthropod taxa that are adapted to utilize the wood subcommunity as an early season overwintering site require other pear or non-pear habitats for feeding and reproduction. In addition, sap feeding scale insects mature and newly hatching nymphs move primarily to leaves and fruit to feed. Thus, both the wood overwintering and wood sap feeding guilds are strongly influenced by life history aspects of community organization. The decline in arthropod biomass in the wood subcommunity in the spring and summer occurs despite an increase in the abundance of the wood subcommunity habitat especially the new green wood (W1).

Subsystem Concordance and Interpenetration: Life history and Trophic Aspects

As recognized by Pimm and Lawton (1981) and indicated in this study, subsystems of arthropod communities are not isolated, but rather intergrade or are interconnected. Interpenetration of subcommunities can be provided by phytophagous arthropods that feed in more than one subcommunity. During a single sample period, Epitremus pyri, Eriophyes pyri, Aspidiotus perniciosus, Psylla pryricola and a few other species may be members of phytophagous guilds in more than one subcommunity. Interpenetration is also provided by arthropods that move from one subcommunity to another during the course of community development. In addition to those mentioned above, a number of other species including Lecanium corni and Tydeus sp. may move from feeding in one subcommunity habitat to another during the course of seasonal habitat development. For example, from early season to expanded leaf, Lecanium scale develop on pear wood, during the summer scale crawlers feed on leaves, and as fall approaches move back to the wood to start this pattern over. Some species utilize more than one subcommunity habitat as a result of the requirements associated with each lifestage. For example, the codling moth, Cydia pomonella, overwinters on the wood subcommunity as a mature larva in a cocoon. After pupation the adults may be associated with the fruit sugar and water guild. Eggs are laid on either the leaves or fruit and the developing larvae comprise the major portion of the fruit boring guild. Several other arthropod species (e.g. leafrollers, some weevils, thrips, mites, etc.) overwinter in various lifestages on the older parts of the wood subcommunity habitat, but as the season progresses move to the developing fruit and/or leaf subcommunities to feed or deposit eggs.

In pear (Figure 2d) and in Scotch broom (Figure 8d) there exist a wide array of carnivorous arthropods that appear to function as generalist predators, taking their prey from a number of community subsystems. In this way they effectively interrelate the dynamics of phytophagous populations from different systems and thereby help couple the systems composing the community. Each of the many species of generalist predators may have little effect on the abundance of a particular prey population but together through "diffuse predation" they may significantly influence its density. Phytophagous arthropods of one or several guilds may serve as additional or alternate prey for predators and so influence their colonization and abundance. Scavenger and fungus feeding mites in pear may serve as alternate prey for predaceous mites which primarily feed on pit feeding eriophyid or tetranychid mites. Similar relationships have been reported by Huffaker and Kennet (1956) and Flaherty (1969).

Through predation, herbivory and other trophic relationships, species populations in each subcommunity are incorporated into one or more systems of populations. Feeding relationships, in concert with habitat and with life history aspects of organization, determine the kinds, abundance and distribution of herbivore guilds. Preying upon each phytophagous guild is a guild of parasitoids and/or specialized predators and preying upon some guilds of parasitoids are hyperparasitoids. In pear these carnivore guilds have not been extensively investigated and, thus, many of the systems of populations are not well defined (Figures 2a-c). However, drawing on Waloff's (1968) work in Scotch broom, particularly her extensive discussion of trophic relationships and habitat requirements, it appears that arthropod subcommunities can be understood as a single, complex system of populations (main stems and branches, Figure 8c) or composed of several relatively discrete systems of populations (seed pods, Figure 8a; foliage and young stems, Figure 8b). The abundance of arthropods in each phytophagous guild may be influenced by their interaction with these specialized carnivores.

Roots' (1973) illustration of the foliage subcommunity on collards provides further support for recognition of trophically organized systems of populations. On collard foliage there are three systems of populations: a pit feeder system, a sap feeder system, and a strip feeder system (Liss et al. 1982).

One system of populations or subcommunity may affect another through effects on its habitat. In pear, the effect of arthropods in the leaf subcommunity on leaves may bring about changes in the fruit - the habitat of another subcommunity - and so affect the fruit subcommunity by altering its food base. For example, leaf injury induced by spider mite feeding can extensively reduce fruit set the following year (Westigard et al. 1964). Feeding on leaves by large numbers of eriophyid mites, as was the case in this study, may reduce both shoot growth (W1 wood) and fruit set.

The effect of arthropod feeding on a particular subcommunity habitat also may induce chemical changes in nearby portions of the same subcommunity habitat. Insect feeding may induce physiological changes in hosts that alter either their nutritional suitability or defensive chemistry, and so influence the dynamics of other individuals of the same or different species (Croft and Heying 1977, Hankioja and Niemela 1979, Hankioja 1980, McClure 1977, 1979, 1980, 1983, McIntyre 1980, Whitham 1981, Ryan 1983, Rhoades 1979, 1983). A competing herbivore may influence the growth and reproduction of others by spatially excluding them from optimal resources on the host plant. *Tiorinia externa* was shown to exclude another species of scale, *Tougaspidiotus tsugae* from utilizing the nutritionally superior young pine needles (McClure 1983). It also is possible that members of a particular guild may affect each other through "diffuse" competition (MacArthur 1972, Pianka 1974). Raupp and Denno (1983) suggested that although young willow leaves support better growth, development, reproduction and survivorship of *Plagiodera versicolora* larvae and adults, they may be an unfavorable site for some immature stages in part because of their tendency to disappear through the combined feeding activities of *P. versicolora* adults and a complex of other willow defoliators.

The impact of herbivore guilds on the habitat also is influenced by the densities of predators and parasitoids in the guilds preying upon the herbivore guild (Price et al. 1980). Predation and parasitism directly influence individual species, but, in addition, it is possible that predation and parasitism affect the outcome of competition within the guild (Roughgarden and Feldman 1975, Menge and Sutherland 1976, Glasser 1979, Holt 1984), and so indirectly impinge upon the abundance of particular populations.

Influence of the Species Pool

Arthropod community organization and development is influenced not only by the development of the habitat but also by the organization of the species pool (Kogan 1981, Lawton 1982, Liss et al. 1982, Moran and Southwood 1982, Southwood et al. 1982, Banerjee 1982, 1983). The kinds, abundance and time of arrival of colonists in pear is, in part, determined by their interactions with habitats and with arthropods outside the pear system. Species pool organization plays an important role in determining the dynamics of the general predator complex associated with pear in southern Oregon (Gut et al. 1982). The phenology of predators and parasitoids may be influenced by the availability of nectar and other food sources, or by the kinds and density of prey encountered in non-pear habitats (Westigard 1973). A number of phytophagous arthropods may utilize non-pear habitats for feeding, overwintering, reproduction, shelter and/or protection from natural enemies (Yothers 1934, Bethell 1978, Fye 1983).

Like the communities they are environments of, species pools are systems that have structure, organization, and development. They can be conceptualized as a system of communities each developing on a community habitat. In southern Oregon, pear grows in a number of locations that differ in the kinds of plant habitats that surround them and, thus, species pool organization varies. Initial investigations of arthropod communities at different locations have been encouraging and results will be presented in detail in a subsequent paper. In general, species pool organization appears to be an important determinant of seasonal changes in the kinds and number or biomass of community subsystems (i.e. the community developmental pattern).

CONCLUSIONS

Arthropod community development in pear can be understood to entail changes in the kinds, number or biomass and spatial distribution of species populations, guilds, systems of populations and subcommunities. Both the development of the community habitat and the organization of the species pool determine changes in arthropod community structure and organization. The influence of seasonal habitat development has been emphasized in this study. The addition, loss, or development of species populations, guilds and subcommunities can be related to the seasonal development of leaf, fruit and wood subcommunity habitats. The role or importance of the habitat is complemented by life history and trophic aspects of community organization and development. Integration of community subsystems is an important element of community organization and, in pear, feeding by phytophagous and predaceous generalists appears to be an important way in which arthropod subcommunities are interrelated.

The developing pear community is part of a more encompassing system of communities. It is from this species pool that arthropods colonize pear. In a given species pool, a community will exhibit different developmental patterns if its habitat has different developmental patterns. Communities in different species pools will exhibit different developmental patterns even if their habitats have the same developmental pattern (Liss et al. 1982).

LITERATURE CITED

Allen, T.F.H. and T.B. Starr. 1982. Hierarchy: Perspectives for ecological complexity. Univ. Chicago Press, Chicago. 310 p.

Banerjee, B. 1981. An analysis of the effect of latitude, age and area on the number of arthropod pest species of tea. J. Appl. Ecol. 18:339-342.

Banerjee, B. 1983. Arthropod accumulation on tea in young and old habitats. Ecol. Entomol. 8:117-123.

Borror, D.J., D.M. DeLong, and C.A. Triplehorn. 1976. An introduction to the study of insects. Holt, Rinehart and Winston, N.Y. 852 p.

Burts, E.C. 1983. Effectiveness of a soft-pesticide program on pear pests. J. Econ. Entomol. 76:936-941.

Burts, E.C. and A.H. Retan. 1973. Detection of pear psylla. Wash. State Ext. Manual 3069.

Carroll, D.P. and S.C. Hoyt. 1984. Natural enemies and their effects on apple aphid, *Aphis pomi* DeGeer (Homoptera: Aphididae), colonies on young apple trees in central Washington. Environ. Entomol. 13:469-481.

Challice, J.S. 1969. Studies on the nature, distribution and biosynthesis of phenolic compounds in *Pyrus* and *Malus*. M.Sc. thesis: Bath University.

Challice, J.S. 1972. Chemotaxonomic studies in *Pyrus* and related genera. Ph.D. thesis: University of Bristol.

Challice, J.S. and M.N. Westwood. 1973. Phenolic compounds of the genus *Pyrus*. IV. Phytochemistry 11:37-44.

Connell, J.H. 1980. Diversity and the coevolution of competition, or the ghost of competition past. Oikos 35:131-138.

Connor, E.F. and D. Simberloff. 1979. The assembly of species communities: chance or competition? Ecology 60:1132-1140.

Croft, B.A. and S.A. Hoying. 1977. Competitive displacement of *Panonychus ulmi* (Acarina: Tetranychidae) by *Aculus schlechtendali* (Acarina:Eriophyidae) in apple orchards. Can. Entomol. 109:1025-1034.

Davis, B.N.N. 1975. The colonization of isolated patches of nettles (Urtica dioica) by insects. J. Appl. Ecol. 12:1-14.

Denno, R.F. and M.S. McClure. eds. 1983. Variable plants and herbivores in natural and managed systems. Academic Press, New York. 717 p.

Ehler, L.E., K.G. Eveleens, and R. van den Bosch. 1973. An evaluation of some natural enemies of cabbage looper on cotton in California. Environ. Entomol. 1:1009-1015.

Elton, C.S. 1966. The pattern of animal communities. London, Methuen. 181 p.

Elton, C.S. and R.S. Miller. 1954. The ecological survey of animal communities: with a practical system of classifying habitats by structural characters. J. Ecol. 42:460-496.

Flaherty, D.L. 1969. Ecosystem trophic complexity and densities of the Willamette mite, Eotetranychus willamettei (Acarina:Tetranychidae). Ecology 50:911-916.

Fye, R.E. 1983. Dispersal and winter survival of the pear psylla. J. Entomol. 76:311-315.

Glasser, J.W. 1979. The role of predation in shaping and maintaining the structure of communities. Am. Nat. 113:631-641.

Gleason, H.A. 1917. The structure and development of the plant association. Bull. Torrey Bot. Club 44:463-481

Gleason, H.A. 1926. The individualistic concept of the plant association. Bull. Torrey Bot. Club 53:331-368.

Gut, L.J., C.E. Jochums, P.H. Westigard, and W.J. Liss. 1982. Variations in pear psylla (Psylla pyricola Foerster) densities in southern orchards and its implications. Acta Horticulturae 124:101-111.

Haukioja, E. 1980. On the role of plant defenses in the fluctuation of herbivore populations. Oikos 35:202-213.

Haukioja, E. and P. Niemela. 1979. Birch leaves as a resource for herbivores: seasonal occurrence of increased resistance in foliage after mechanical damage of adjacent leaves. Oecologia 30:151-159.

Holt, R.D. 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. Am. Nat. 124:377-406.

Hoyt, S.C. 1969. Integrated chemical control of insects and biological control of mites of apple in Washington. J. Econ. Entomol. 62:74-86.

Huffaker, C.B. and C.E. Kennet. 1956. Experimental studies on predation: predation and cyclamen mite populations on strawberries in California. Hilgardia 26:191-222.

Klecka, W.R. 1975. Discriminant analysis. In "SPSS Statistical Package for the Social Sciences" (N.H. Nie, C.H. Hull, J.G. Jenkins, K. Steinbrenner and D.H. Bent, eds.), McGraw Hill, N.Y. pp. 434-467.

Kogan, M. 1981. Dynamics of insect adaptation to soybean: Impact of integrated pest management. Env. Entomol. 10:363-371

Krantz, G.W. 1978. A Manual of Acarology. Oregon State University Book Stores, Inc., Corvallis, Oregon. 509 p.

Lawton, J.H. 1978. Host-plant influences on insect diversity: the effects of space and time. In "Diversity of Insect Faunas" (L.A. Mound and N. Waloff, eds.) pp. 105-125.

Lawton, J.H. 1982. Vacant niches and unsaturated communities: a comparison of bracken herbivores at sites on two continents. J. Ecol. 51:573-595.

Lawton, J.H. 1983. Plant architecture and the diversity of phytophagous insects. Ann. Rev. Entomol. 28:23-39.

Lawton, J.H. and M.P. Hassell. 1981. Asymmetrical competition in insects. Nature 289:793-795.

Lawton, J.H. and D. Schröder. 1977. Effect of plant type, size of geographical range and taxonomic isolation on number of insects associated with British plants. Nature 265:137-140.

Lawton, J.H. and D.R. Strong. 1981. Community patterns and competition in folivorous insects. Am. Nat. 118:317-338.

Liss, W.J., L.J. Gut, P.H. Westigard, and C.E. Warren. 1982. A perspective for understanding arthropod community organization and development in pear. Acta Horticulturae 124:85-100.

Liss, W.J. and C.E. Warren. 1980. Ecology of aquatic systems. In "Fisheries Management" (R.T. Lackey and L.A. Nielsen, eds.), John Wiley, New York. pp. 41-79.

MacArthur, R.H. 1972. Geographical Ecology; patterns in the distribution of species. Harper and Rowe, New York. 269 p.

MacArthur, R.H. and E.O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, N.J. 203 p.

Madsen, H.F., P.H. Westigard, and R.L. Sisson. 1963. Observations on the natural control of pear psylla, Psylla pyricola Foerster, in California. Can. Entomol. 95:837-844.

Mayse, M.A. and P.W. Price. 1978. Seasonal development of soybean arthropod communities in east central Illinois. Agro-Ecosystems 4:387-405.

McClure, M.S. 1979a. Self-regulation in populations of the elongate hemlock scale, Fiorinia externa (Homoptera: Diaspididae). Oecologia 39:25-36.

McClure, M.S. 1979b. Self-regulation in hemlock scale populations: role of food quantity and quality. Misc. Publ. Entomol. Soc. Am. 11:33-40.

McClure, M.S. 1980a. Foliar nitrogen: a basis for host suitability for elongate hemlock scale, Fiorinia externa (Homoptera: Diaspididae). Ecology 61:72-79.

McClure, M.S. 1980b. Competition between exotic scales: scale insects on hemlock. Ecology 61:1391-1401.

McClure, M.S. 1983. Competition and increased resource heterogeneity. In "Variable Plants and Herbivores in Natural and Managed Systems" (R.F. Denno and M.S. McClure, eds.), Academic Press, New York. pp. 125-153.

McIntyre, J.L. 1980. Defenses triggered by previous invaders: nematodes and insects. In "Plant Disease: an Advanced Treatise" (J.G. Harsfall and E.B. Cowling, eds.), Vol. 5. Academic Press, New York. pp. 333-343.

McMullen, R.D. 1964. Biological control of pear psylla. Washington State Hort. Assoc. Proc. 60:79-82.

Menge, B.A. and J.P. Sutherland. 1976. Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. Am. Nat. 100:351-369.

Messenger, P.S., E. Biliotti, and R. van den Boxch. 1973. The importance of natural enemies in integrated control. In "Theory and Practice of Biological Control" (C.B. Huffader and P.S. Messenger, eds.), Academic Press, New York. pp. 543-563.

Moran, V.C. 1980. Interactions between phytophagous insects and their Opuntia hosts. Ecol. Entomol. 5:153-164.

Moran, V.C. and T.R.E. Southwood. 1982. The guild composition of arthropod communities in trees. J. Anim. Ecol. 51:289-306.

Oatman, E.R. and G.R. Platner. 1969. An ecological study of insect populations on cabbage in southern California. Hilgardia 40:1-40.

Pianka, E.R. 1974. Niche overlap and diffuse competition. Proc. Natl. Acad. Sci. U.S. 71:2141-2145.

Pimental. R.A. 1979. Morphometrics, the Multivariate Analysis of Biological Data. Kendall/Hunt, Dubuque, Iowa 276 p.

Pimm, S.L. and J.H. Lawton. 1980. Are food webs divided into compartments? J. Anim. Ecol. 49:879-898.

Price, P.W. 1976. Colonization of crops by arthropods: non-equilibrium communities in soybean fields. Env. Entomol. 5:605-611.

Price, P.W. 1983. Hypotheses on organization and evolution in herbivorous insect communities. In "Variable Plants and Herbivores in Natural and Managed Systems" (R.F. Denno and M.S. McClure, eds.), Academic Press, New York. pp. 559-596.

Price, P.W. 1984. Communities of specialists: Vacant niches in ecological and evolutionary time. In "Ecological Communities Conceptual Issues and the Evidence" (D.R. Strong, D. Simberloff, L.G. Abele, and A.B. Thistle, eds.), Princeton University Press, Princeton. pp. 510-523.

Price, P.W., C.E. Bouton, P. Gross, B.A. McPheron, J.N. Thompson, and A.E. Weis. 1980. Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. Ann. Rev. Ecol. Syst. 11:41-65.

Price, P.W. and G.P. Waldbauer. 1982. Ecological aspects of pest management. In "Introduction to Insect Pest Management" 2nd Ed. (R.L. Metcalf and W.H. Luckman, eds.), John Wiley and Sons, New York. pp. 33-68.

Rathcke, B.J. 1976. Competition and coexistence within a guild of herbivorous insects. Ecology 57:76-87.

Raupp, M.J. and R.F. Denno. 1983. Leaf age as a predictor of herbivore distribution and abundance. In "Variable Plants and Herbivores in Natural and Managed Systems" (R.F. Denno and M.S. McClure, eds.), Academic Press, New York. pp. 91-124.

Rey, J.R. 1981. Ecological biogeography of arthropods on Spartina islands in northwest Florida. Ecol. Monographs 51:237-265.

Rey, J.R. and E.D. McCoy. 1979. Application of island biogeographic theory to pests of cultivated crops. Environ. Entomol. 8:577-582.

Rhoades, D.F. 1979. Evolution of plant chemical defense against herbivores. In "Herbivores: Their Interaction with Secondary Plant Metabolites" (G.A. Rosenthal and D.H. Janzen, eds.), Academic Press, New York. pp. 3-54.

Rhoades, D.F. 1983. Herbivore population dynamics and plant chemistry. In "Variable Plants and Herbivores in Natural and Managed Systems" (R.F. Denno and M.S. McClure, eds.), Academic Press, New York. pp. 155-221.

Richards, O.W. and R.G. Davies. 1977. Imms' General Textbook of Entomology. Volume 2: Classification and Biology. John Wiley and Sons, N.Y. 1352 p.

Root, R.B. 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (Brassica oleracea). Ecol. Monogr. 43:95-124.

Rosenthal, G.A. and D.H. Janzen, eds. 1979. Herbivores, Their Interaction with Secondary Plant Metabolites. Academic Press, New York. 718 p.

Roughgarden, J. and M. Feldman. 1975. Species packing and predation pressure. Ecology 56:489-492.

Ryan, C.A. 1983. Insect-induced chemical signals regulating natural plant protection responses. In "Variable Plants and Herbivores in Natural and Managed Systems" (R.F. Denno and M.S. McClure, eds.) Academic Press, New York. pp. 43-60.

Simberloff, D.S. 1978. Colonization of islands by insects: immigration, extinction, and diversity. Symp. R. Entomol. Soc. London: 9. pp. 139-153.

Southwood, T.R.E. 1977. Habitat the templet for ecological strategies? J. Anim. Ecol. 46:337-365.

Southwood, T.R.E., V.C. Moran and C.E.J. Kennedy. 1982. The richness, abundance and biomass of the arthropod communities on trees. J. Anim. Ecol. 51:635-649.

Strong, Jr., D.R. and D.A. Levin. 1979. Species richness of plant parasites and growth of their host. Am. Nat. 114:1-22.

Waloff, N. 1968. Studies on the insect fauna on Scotch broom Sarcothamnus scoparius (L.) Wimmer. Adv. Ecol. Res. 5:87-208.

Warren, C.E., M.W. Allen and J.W. Haefner. 1979. Conceptual frameworks and the philosophical foundations of general living systems theory. Behav. Sci. 24:296-310.

Westigard, P.H. 1973. The biology of and effect of pesticides on Deraeocoris brevis piceatus (Heteroptera: Miridae). Can. Entomol. 105:1105-1111.

Westigard, P.H. 1979. Integrated pest management of insects and mites of pear. In "Pest Management Programs for Deciduous Tree Fruits and Nuts" (D.J. Boethel and R.D. Eikenbary, eds.), Plenum Press, New York. pp. 151-202.

Westigard, P.H., L. Gentner and B.A. Butt. 1975. Codling Moth: Egg and first instar mortality on pear with special references to varietal susceptibility. Environ. Entomol. 5:51-54.

Westigard, P.H., P.B. Lombard, R.B. Allen and J.G. Strang. 1980. Pear psylla: population suppression through host plant modification using diaminozide. Environ. Entomol. 9:275-277.

Westigard, P.H., P.B. Lombard, and J.H. Grim. 1966. Preliminary investigations of the effect of feeding of various levels of two-spotted spider mite on its anjou pear host. Amer. Soc. Hort. Sci. 89:117-122.

Westigard, P.H., M.N. Westwood, and P.B. Lombard. 1970. Host preference and resistance of *Pyrus* species to the pear psylla, *Psylla pyricola* Foerster. J. Amer. Soc. Hort. Sci. 95:34-36.

Westwood, M.N. and P.H. Westigard. 1969. Degree of resistance among pear species to the woolly pear aphid, *Eriosoma pyricola* J. Amer. Soc. Hort. Sci. 94:91-93.

Whitham, T.G. 1981. Individual trees as heterogeneous environments: Adaptation to herbivory or epigenetic noise? *In* "Insect Life History Patterns: Habitat and Geographic Variation" (R.F. Denno and H. Dingle, eds.), Springer-Verlag, Berlin/New York. pp. 9-27.

Wieres, R.W. and H.C. Chiang. 1973. Integrated control of prospects of major cabbage insect pests in Minnesota-Based on the faunistic host varietal, and trophic relationships. Univ. Minn. Agr. Exp. Sta. Tech. Bull. 291. 42 p.

Yothers, M.A. 1934. Biology and control of tree hoppers injurious to fruit trees in the pacific northwest. U.S.D.A. Tech. Bull. 402. 46 p.