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Invertebrate and Microbial Associates

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7.1 INTRODUCTION

Coincident with and immediately subsequent to bark penetration, colonization and establishment of bark beetle and pathogen populations in the host, a myriad of associated organisms that are intimately associated with the bark beetles arrives at and finds access to the subcortical environment of infested trees. Although many of these associated species have been identified and cataloged, relatively little is known about the biology or impact of most species. Evaluation of the effects of associated species is difficult for a variety of reasons, including the wide expanse of taxonomic categories (ranging from pathogenic bacteria to arthropod parasitoids to avian vertebrate predators) and ecological groupings that encompass all aspects of multiple species interactions. In addition, the cryptic habit of these organisms within their hosts confounds efforts to sample and even to observe. As a result of these research difficulties, the importance of associates in promotion or natural control of bark beetles and pathogens may be underestimated. The perception that associated species have little effect cannot be supported or rejected unless research in this area is encouraged. This

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chapter focuses on the effects of associated species on the survival and reproduction of bark beetles and pathogens.

7.2 ORGANISMS INVOLVED

Researchers have been aware of the many associated organisms in bark beetle-infested trees for some time (Shelford, 1913; Blackman and Stage, 1924; Savely, 1939) and have noted that their importance relates to the variety of roles they play in the successional process of tree death and decomposition. Taxonomic inventories (some more extensive than others) of associates have been compiled for many of the primary bark beetles, including most species of *Dendroctonus* and some species of *Ips* and *Scolytus* (Table 7.1). Table 7.1 is not intended to be a complete inventory of all published literature, but does represent the majority of current North American information.

Some associated species are host-tree specific. However, the roles of most related species are similar across tree taxa, permitting a functional classification based on these roles. One approach to classification of the ecological groups of organisms associated with bark beetles in North American conifers is shown in Fig. 7.1. Characteristics of each group and examples of the organisms in each category are discussed below.

7.2.1 Bark beetle predators

Most information on bark beetle predators comes from studies of predation in beetle galleries or on the bark surface of beetle-infested trees (Dahlsten, 1982). Predation of bark beetles flying from tree to tree is poorly known.

Examination of the predaceous arthropod families and genera listed in Table 7.1 reveals that many are common to several of the bark beetles, and some to nearly all. Predaceous

Fig. 7.1. Bark beetle/associate ecological relationships, with examples of organisms comprising specific groups

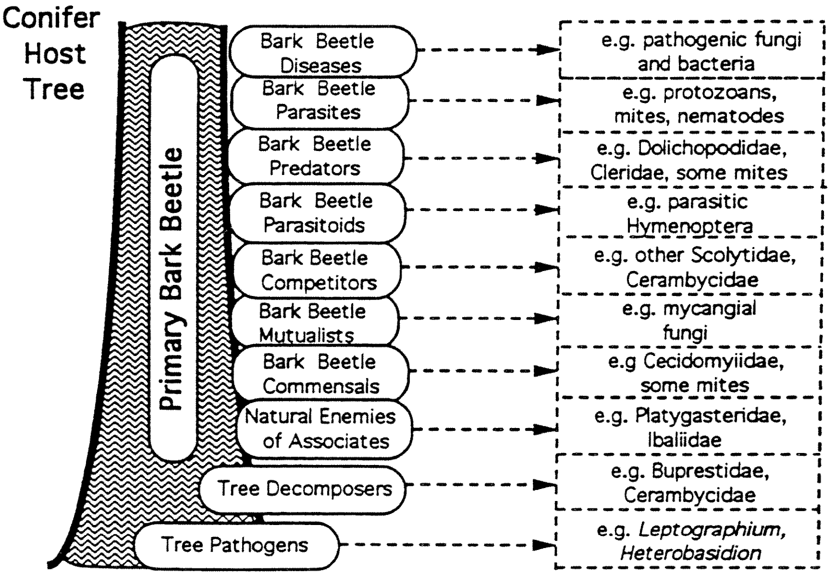


Table 7.1. Arthropod families and genera recorded as associates of conifer-infesting *Dendroctonus Scolytus*, and *Ips* bark beetles in North America

	Dendroctonus							*Scolytus*								*Ips*											
	Df[a]	Db	Dp	Da	Dps	Dr	Ds	Sa	Sl	Sp	Spr	Ss	St	Su	Sv	Ia	Ic	Ig	Ib	Ip	Ico	Iac	Ipi	Ipe	Il	Im	Ipl
Hemiptera																											
Anthocoridae																											
Lyctocoris	x	x		x	x																						
Scoloposcelis	x	x	x													x	x	x		x			x				
Aradidae																											
Aradus	x	x		x																							
Coleoptera																											
Histeridae				x	x																						
Plegaderus	x	x	x																	x						x	
Platysoma	x	x	x				x																				
Staphylinidae				x	x	x																					
Aleocharinae																				x							x
Nudobius	x	x	x																					x		x	x
Quedius																									x		
Buprestidae	x																										
Buprestis		x	x	x																							
Melanophila		x	x																								
Chrysobothris		x	x																								
Dermestidae	x		x																								
Ostomidae																											
Temnochila	x	x	x	x	x										x												
Tenebriodes	x	x		x	x																						
Corticotomus	x																										
Cleridae						x																					
Thanasimus	x		x		x	x																					
Enoclerus		x	x	x	x	x								x	x	x	x	x		x				x			x
Cymatodera		x	x																								
Nitidulidae																											
Epuraea	x		x	x																							
Glischrochilus			x	x																							
Soronia		x		x																							

Table 7.1 continued

	Dendroctonus							*Scolytus*								*Ips*											
	Df[a]	Db	Dp	Da	Dps	Dr	Ds	Sa	Sl	Sp	Spr	Ss	St	Su	Sv	Ia	Ic	Ig	Ib	Ip	Ico	Iac	Ipi	Ipe	Il	Im	Ipl
Bostrichidae			x																								
Rhizopgagidae																											
Rhizophagus	x	x	x	x		x	x							x													
Cucujidae																											
Cucujus		x	x																								
Silvanus	x	x	x																								
Lathridiidae	x																										
Corticaria		x	x																								
Colydiidae																											
Aulonium	x	x	x	x																							
Lasconotus	x	x	x	x	x									x	x					x							x
Colydium	x	x																									
Othniidae					x																						
Othnius		x	x	x																							
Tenebrionidae																											
Corticeus	x	x	x	x	x	x								x													
Melandryidae																											
Rushia		x	x	x	x																						
Serropalpus		x	x												x												
Throscidae																											
Triagus	x			x																							
Cerambycidae																											
Acanthocinus	x	x	x	x																							
Monochamus	x		x													x	x	x					x				
Asemum	x		x	x																							
Anoplodera			x																								
Stenocorus			x	x																							
Megasemum			x	x																							
Xylotrechus			x	x											x												
Spondylis		x	x																								
Callidium		x	x																								

	Dendroctonus							*Scolytus*								*Ips*											
	Df[a]	Db	Dp	Da	Dps	Dr	Ds	Sa	Sl	Sp	Spr	Ss	St	Su	Sv	Ia	Ic	Ig	Ib	Ip	Ico	Iac	Ipi	Ipe	Il	Im	Ipl
Curculionidae																											
Cossonus	x	x	x																								
Platypodidae																											
Platypus	x	x		x													x	x					x				
Scolytidae																											
Dendroctonus	x	x	x	x												x	x	x		x							
Scolytus															x												
Ips	x	x	x	x												x	x	x					x				
Pseudohylesinus															x												
Hylastes	x	x		x												x	x	x									
Pityokteines		x	x												x												
Orthotomicus			x	x																							
Pityogenes			x	x														x									
Hylurgops		x	x	x																							
Xyleborus		x		x																							
Pityophthorus	x	x	x												x												
Crypturgus	x		x												x			x									
Gnathotrichus	x	x		x												x	x	x					x				
Diptera																											
Sciaridae																											
Bradysia		x	x	x																							
Cecidomyiidae																											
Lestodiplosis	x		x																								
Winnertzia	x	x																									
Stratiomyidae					x																						
Zabrachia	x	x	x			x	x																				
Scenopinidae			x		x																						
Empididae					x																						
Drapetis	x	x	x																								
Tachypeza		x	x																								

Table 7.1 continued

	Dendroctonus							*Scolytus*								*Ips*											
	Df[a]	Db	Dp	Da	Dps	Dr	Ds	Sa	Sl	Sp	Spr	Ss	St	Su	Sv	Ia	Ic	Ig	Ib	Ip	Ico	Iac	Ipi	Ipe	Il	Im	Ipl
Dolichopodidae																											
Medetera	x	x	x		x	x	x							x	x			x		x			x	x			x
Phoridae																											
Megaselia		x	x												x												
Lonchaeidae																											
Lonchaea	x	x	x		x	x								x	x												
Xylophagidae																											
Xylophagus																								x			
Hymenoptera																											
Siricidae																											
Sirex		x	x	x														x									
Ichneumonidae																											
Gelis		x	x																								
Xorides															x												
Braconidae																											
Bracon																							x				
Coeloides	x	x	x	x	x	x								x	x	x	x	x		x	x		x	x			x
Atanycolus	x	x		x										x							x						
Dendrosoter	x	x	x	x						x						x		x		x	x		x				
Doryctes	x	x																									
Meteorus	x	x	x																								
Chelonus	x	x																									
Orgilus																					x						
Spathius	x						x	x	x	x			x	x	x	x		x		x			x		x		
Cosmophorus			x				x																				
Heterospilus											x					x		x					x				
Ecphylus									x			x		x	x												
Stephanidae																											
Schlettererius		x	x																								
Eulophidae																											
Tetrastichus	x	x																									

	Dendroctonus							*Scolytus*								*Ips*											
	Df^a	Db	Dp	Da	Dps	Dr	Ds	Sa	Sl	Sp	Spr	Ss	St	Su	Sv	Ia	Ic	Ig	Ib	Ip	Ico	Iac	Ipi	Ipe	Il	Im	Ipl
Thysanidae																											
Signophora	x	x																									
Encrytidae																											
Avetianella		x	x																								
Eupelmidae																											
Eupelmus	x	x														x			x								
Lutnes	x		x																								
Torymidae																											
Crodontomerus																	x										
Roptrocerus	x	x	x		x	x	x								x	x	x	x		x	x		x	x			x
Pteromalidae																											
Tomicobia		x			x											x	x	x			x		x				
Cheiropachus		x			x					x				x	x												
Coelopisthia																								x			
Macromesus		x	x								x			x	x					x							
Amblymerus		x	x																		x		x				
Rhopalicus	x	x	x				x				x			x		x		x		x			x				x
Heydenia	x	x	x				x							x		x		x					x				
Dinotiscus	x	x	x	x	x	x								x	x	x	x	x		x	x		x	x			x
Eurytomidae																											
Eurytoma	x	x	x					x						x		x		x		x	x		x				
Ibaliidae																											
Ibalia		x	x																								
Scelionidae																											
Telenomus	x	x																									
Ceraphronidae																											
Ceraphron	x	x																									
Platygasteridae																											
Leptacis	x	x																									
Platygaster	x	x	x																								

Table 7.1 continued

	Dendroctonus							*Scolytus*								*Ips*											
	Df[a]	Db	Dp	Da	Dps	Dr	Ds	Sa	Sl	Sp	Spr	Ss	St	Su	Sv	Ia	Ic	Ig	Ib	Ip	Ico	Iac	Ipi	Ipe	Il	Im	Ipl
Formicidae																											
Camponotus	x	x	x	x																							
Leptothorax	x		x																								
Monomorium	x			x																							
Formica			x	x																							
Sphecidae																											
Passaloecus		x	x																								
TOTAL TAXA	61	75	74	41	21	12	9	2	2	2	3	1	1	16	21	18	13	22	1	16	9	0	19	7	1	2	10

[a] Df = *D. frontalis*, Db = *D. brevicomis*, Dp = *D. ponderosae*, Da = *D. adjunctus*, Dps = *D. pseudotsugae*, Dr = *D. rufipennis*, Ds = *D. simplex*, Sa = *S. abietis*, Sl = *S. laricis*, Sp = *S. piceae*, Spr = *S. praeceps*, Ss = *S. subscaber*, St = *S. tsugae*, Su = *S. unispinosus*, Sv = *S. ventralis*, Ia = *I. avulsus*, Ic = *I calligraphus*, Ig = *I grandicollis*, Ib = *I borealis*, Ip = *I. paraconfusus*, Ico = *I confusus*, Iac = *I. acuminatus*, Ipi = *I. pini*, Ipe = *I. perturbatus*, Il = *I. latidens*, Im = *I. mexicanus*, Ipl = *I. plastographus*.

insects known to feed on bark beetles are primarily members of the families Anthocoridae (Heteroptera), Formicidae (Hymenoptera), Histeridae, Staphylinidae, Ostomidae (=Trogositidae), Cleridae, Rhizophagidae, Cucujidae, Colydiidae, Othniidae, Tenebrionidae, Melandryidae (Coleoptera), Stratiomyidae, Empididae, Dolichopodidae and Lonchaeidae (Diptera). In addition to predaceous insects, birds, and perhaps spiders, are important predators of bark beetles prior to bark penetration (Dahlsten, 1982).

The degree of host specificity for most species in these families is uncertain. Many prey on other members of the vast complex of associated organisms in addition to the primary bark beetle host.

7.2.2 Bark beetle parasitoids

Parasitoids differ from predators in that they do not kill their prey directly but deposit eggs or larvae on the selected prey. The offspring subsequently consume and kill the prey during their development. Parasites, by contrast, usually do not kill their hosts (Dahlsten, 1982). All parasitoids of bark beetles are wasps (Hymenoptera). Parasitoid species most commonly associated with bark beetles are members of the families Braconidae, Eulophidae, Eupelmidae, Torymidae, Pteromalidae, and Eurytomidae. Parasitoids are an important and diverse group of bark beetle associates. The total number of associated parasitoid species is not known exactly for any of the bark beetles, because the host relationships of many of the uncommon potential parasitoids have not been investigated. Many of these species are quite host specific, whereas others attack both the primary bark beetle and scolytids that are potential competitors (Berisford, 1974).

Sorting out the biology of this parasitoid complex has been recognized as an extremely demanding and difficult task. For many parasitoid species the host relationships are uncertain, and there may be more species and/or varieties than previously thought (Espelie *et al.*, 1990). However, some genera are common to most bark beetle species, probably interacting similarly among hosts. Generally, the bark beetle species of greatest economic importance are those for which classification of the associates has been most thorough. As in-depth studies are conducted with the less well known beetles, undoubtedly a greater diversity of parasitoids will be encountered, and the consistency with which some parasitoid species are found on several beetle taxa will increase.

7.2.3 Bark beetle parasites and diseases

Organisms parasitic on bark beetles include nematodes, mites, and protozoans. Massey (1974) summarized the biology and taxonomy of nematodes associated with North American bark beetles. Reviews by Dahlsten (1982) and Mills (1983) provide a good source of literature relating to various parasites and their impact on bark beetles. Diseases, including those caused by bacteria, fungi, nematodes, protozoa and possibly viruses, may be important factors regulating populations of *D. frontalis* (Moore, 1971; Sikorowski *et al.*, 1979). Nematodes have been reported to reduce fertility and fecundity in *D. frontalis* and *D. pseudotsugae* (Thong and Webster, 1975; Kinn, 1980). Hoffard and Coster (1976) found four species of nematodes infecting three southern *Ips* spp. in Texas. Infection delayed emergence of adults but had little effect on reproduction. Mills (1983) noted that the fungal pathogen *Beauvaria bassiana* has been reported from *Ips amitinus* and *I. typographus* in Europe.

7.2.4 Commensals

Commensals (organisms that benefit from, but do not affect, their associate) are represented by a large and diverse assemblage of taxa whose biology and relationship to bark beetles, and the phloem-inhabiting guild as a whole, are poorly known. Many of the mites discussed below are commensal. Lindquist (1969) reviewed the tarsonemid mite associates of *Ips* and related bark beetles. Other commensals include fungivorus dipterans and coleopterans, many of whom are listed in Table 7.1.

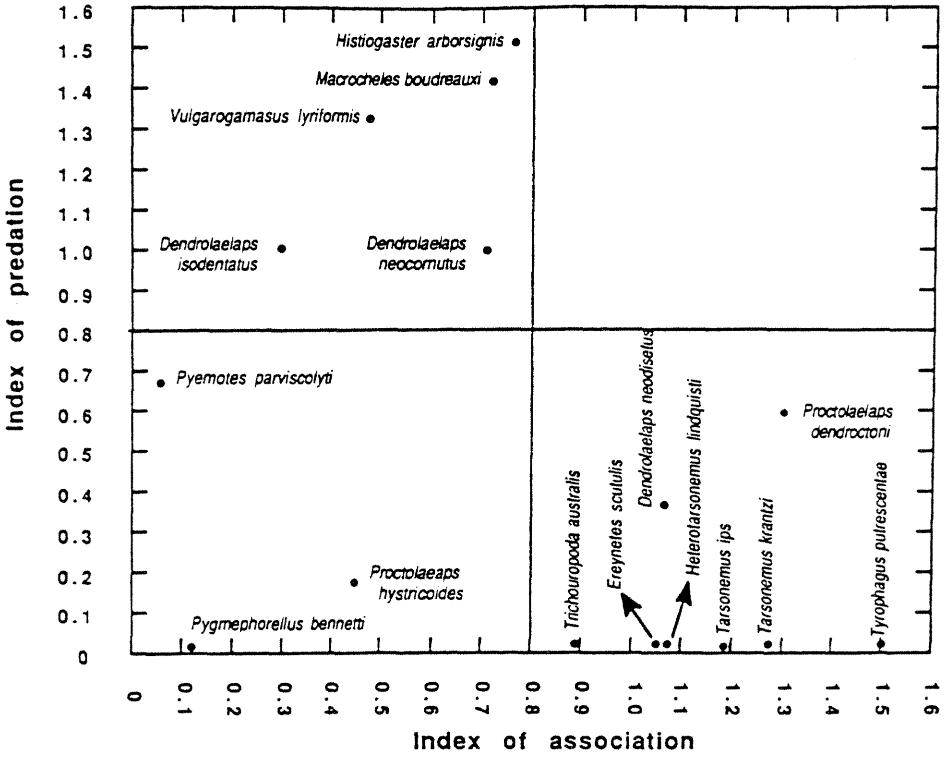
A vast complex of mites is found with pine bark beetles in their host trees (Fig. 7.2). The role of different species varies extensively and is unknown for many. Unlike most insect associates of bark beetles, mites are wingless. This requires that individuals ride on beetle hosts or other flying associates (phoresy) in order to disperse to new hosts. A phoretic relationship ensures dispersal to new subcortical habitats but does not necessarily imply that the mite interacts with the beetle in any other way. The majority of mites have little or no effect on the bark beetles with which they are associated. Fig. 7.3, devised by Wilson (1980),

Fig. 7.2 A variety of predacious and saprophytic mites, such as the fungus-feeding acarids (probably *Histiogaster* sp.), are associated with bark beetle tunnels, commonly reaching new hosts by riding on dispersing beetles.

depicts a unique method for evaluating the effect of mites on *D. frontalis*. This relationship is based on data from Kinn and Witcosky (1978), Moser (1975, 1976), and Moser and Roton (1971). The figure shows that the closer the phoretic relationship between a mite and *D. frontalis* (as measured by the index of association), the less threat that mite is to the beetle. Thus, mite species with a low index of association possess high probabilities for predation on *D. frontalis*, whereas mites with a high index are benign. In fact, none of the mites phoretic on *D. frontalis* substantially harm its brood, except certain mite species when starved (Moser, 1975; Wilson, 1980).

The phoretic latitude (number of animal species that a mite will ride) varies with each particular mite species. Although mite parasitoids tend to be the most specific, practically all ride more than one host species. An exception to this may be *Pyemotes parviscolyti*. So far, this mite is known to ride only *Pityophthorus annectans* (called *P. bisulcatus* in Moser *et al.*, 1971), a common but inconspicuous bark beetle infesting small branches of southern pines. One other mite that appears to be specific to a single bark beetle is *Ereynetes sinescutulis* which is known to ride only *Ips pini* (Hunter *et al.*, 1989). However, like many other mites recorded from single species, the biology of this species is incompletely known, and more collecting may broaden its phoretic latitude. Many species of the egg-parasitic genus *Iponemus* generally ride only one species of *Ips* (Lindquist, 1969). However, the three species in the southern pine subcortical habitat each tend to make "mistakes," riding one of the other two *Ips* species (but never *D. frontalis*) about 5–10% of the time (J. C. Moser, unpublished).

Fig. 7.3. Relationship between the relative closeness of association of mites and *D. frontalis* and the observed degree of predation of those mites on *D. frontalis*. (J.C. Moser data, adapted from Wilson, 1980.)



Other mites ride closely related species of bark beetles. *Tarsonemus krantzi* seems to be restricted to certain members of the *D. frontalis* species group (Lanier *et al.*, 1988), having been found so far on *D. frontalis, D. mexicanus,* and *D. adjunctus*, but not *D. brevicomis*. *Proctolaelaps hystrix, Histiostoma media,* and *Tarsonemus "terebrans"* are phoretic on the "turpentine" species group of *Dendroctonus*, i.e. *D. rhizophagus, D. terebrans,* and *D. valens*. *Elattoma* n. sp. #9 has a somewhat broader latitude, riding only *D. frontalis* and *D. terebrans* in the southern pine habitat, but never *Ips grandicollis*, one of the three species of *Ips* in this habitat.

The Holarctic species *Iponemus gaebleri* apparently rides all species of *Ips* that infest *Picea*, with one subspecies exploiting an *Ips* that attacks *Pinus* (Lindquist, 1969). *Pyemotes scolyti* is a classic example of a parasite specific to a particular genus of bark beetles, *Scolytus*. Thus *P. scolyti* can be found in subcortical habitats as diverse as *Ulmus*, *Pseudotsuga*, and *Prunus*. Members of the genus *Mucroseius* and perhaps species of a few other genera are phoretic only on cerambycid beetles (Kinn and Linit, 1989). *Cercoleipus coelonotus* is restricted to the genus *Ips*, but only the larger species. This is understandable because *C. coelonotus* is the largest mite associated with bark beetles, approaching the size of many tick deutonymphs. In the southern pine subcortical habitat, *C. coelonotus* rides only *Ips calligraphus*, the largest of the three species of *Ips*. Under experimental conditions, *C. coelonotus* rode *D. ponderosae*, but under field conditions this was not seen (Kinn, 1971). In central Louisiana, at least, *Tarsonemus subcorticalis* rides *Ips* and *Monochamus*, but rejects *Dendroctonus* (Kinn and Linit 1989; Moser, unpublished data). The egg parasite, *Paracarophaenax ipidarius* is recorded to ride only under the thorax of *Ips typographus* in Europe. However, in North America (where *I. typographus* does not occur) it occupies this position on *Ips pini, I. paraconfusus* and *I. plastographus* and rides under the elytra of *D. brevicomis* (Kinn, 1971; Moser, unpublished data). As with many species whose biology is poorly known, this disparity of host and phoretic data suggests two or more sibling species.

The vast majority of mites seem to accept any subcortical habitat, riding many of the scolytids and their associates. Of these, the beetle associates carry the most. Two common groups of associates, *Corticeus* spp. (Tenebrionidae) and the Cleridae, may exceed the primary scolytids in the number of individuals and species of mites carried. These subcortical mites include *Histiogaster arborsignis, Histiostoma varia, Mexecheles virginiensis, Paraleius leontonychus, Pleuronectocelaeno drymocoetes, Proctolaelaps fiseri, P. hystricoides, Tarsonemus ips, T. subcorticalis, Trichouropoda australis, Vulgarogamasus lyriformis,* and many others (Moser and Roton, 1971; Moser unpublished data). Some of these mites such as *Histiogaster arborsignis* and *Histiostoma varia* stick to practically any animal under bark (including other mites).

Some of the above mite taxa apparently are restricted to particular regions, perhaps because they have not been introduced to other habitats. Examples include *Macrocheles boudreauxi* and *Proctolaelaps dendroctoni*, which are known only from the southern pine subcortical habitat. *Pyemotes giganticus* has been found with at least 16 species of bark beetles (and one *Corticeus* associate) in western conifers. This mite also rode *D. frontalis*, which is not native to western North America, under experimental conditions (Cross *et al.*, 1981; Moser, 1981).

Some mites commonly seen in subcortical habitats of *Pinus* also may be found in the subcortical habitats of nearby tree species. *Trichouropoda hirsuta* is a mite commonly seen in the southern pine subcortical habitat and is normally phoretic on cerambycids (Kinn and Linit, 1989). However, phoretic deutonymphs also have been found on adults of the tenebrionid *Alobates pennsylvanica* collected from well decomposed stumps of *Liquidambar styraciflua* (J. C. Moser, unpublished).

7.2.5 Competitors

Primary beetle and pathogen species benefit from being the initial organisms to colonize the nutrient-rich phloem tissue of freshly killed conifers. Other phloem-inhabiting species that rapidly locate and colonize this resource include other scolytids, species of the beetle families Cerambycidae and Buprestidae, and various competing fungi and other microorganisms. An example illustrating the structure and dynamics of the phloem-inhabiting insect guild, is seen in the southern *Pinus* community of *D. frontalis*, *Ips* spp. and *Monochamus titillator* (Birch *et al.*, 1980; Coulson *et al.*, 1980; Paine *et al.*, 1981; Miller, 1985; Wagner *et al.*, 1985; Flamm *et al.*, 1987, 1989). In this situation, larvae of the cerambycid *Monochamus* will kill bark beetle larvae by indiscriminate foraging through phloem inhabited by the scolytids, but mortality to the scolytids normally is minimized through niche partitioning, i.e. different colonization and development rates and phloem utilization strategies.

Competing fungi such as *Trichoderma* spp. and *Penicillium* spp. may inhibit colonization and spread of pathogenic fungi. For example, *Trichoderma* prevents growth of *Heterobasidion annosum* and perhaps other pathogenic fungi in conifer stumps (Goldfarb *et al.*, 1989). Competition also occurs among beetle-vectored pathogens. Parmeter *et al.* (1989) reported that coinoculation of *Pinus ponderosa* with isolates of *Leptographium terebrantis* and *Ophiostoma ips* significantly reduced the rate of sapwood penetration observed for *L. terebrantis* alone. Inhibition can occur through production of antibiotic substances that prevent pathogen establishment or growth or through rapid growth and depletion of available resources (Rayner and Todd, 1979).

7.2.6 Mutualists

Mutualists include some mites and many microorganisms. The phoretic mite *Dendrolaelaps neodisetus* benefits *Dendroctonus frontalis* by preying on parasitic nematodes (Kinn, 1980). Many species of bacteria, yeasts and mycelial fungi have been reported to benefit associated conifer-attacking bark beetles. Whitney (1982) lists over 100 examples of microorganisms associated with bark beetles or their habitats in conifers and suggests that many more remain to be discovered. Although the ecological relationships of many of these associations are unknown and remain fruitful topics of investigation, Whitney (1982) gives 12 examples of yeasts and mycelial fungi that are proven or suspected mutualists of conifer bark beetles. Other recent reviews of bark beetle–fungal relationships include Batra (1979) and Beaver (1989).

Dissemination is the primary benefit that the mites and microorganisms receive from their associated beetles. Indeed, many require the penetration of the bark barrier by the host beetles in order to colonize susceptible tree tissues (Schowalter *et al.*, 1991). The pleomorphic (many distinct life stages) growth habit and gelatinous spores of the fungi (Fig. 7.4) represent adaptations for insect transmission; insect vectors are the only known mechanisms for dispersal in some species (Webber and Gibbs, 1989; Chapter 3).

Most of the mutualistic fungi are vectored specifically by certain species of bark beetles, and most are adapted to be transported in the mycangia of their respective vectors. Beaver (1989) and Bright (Chapter 2) discuss the benefits of mutualism and the relationships of beetle mycangia and fungal transmission. Mycangia are not always necessary for a success-

Fig. 7.4. A diverse fungal flora is inoculated rapidly into the subcortical habitat of trees colonized by bark beetles

ful relationship between beetle and fungus. A number of beetle–fungal relationships appear successful without mycangia on the host beetle (Witcosky *et al.*, 1986; Chapter 2). However, at least some species of mycangial fungi are known to undergo differentiation and to reproduce within the mycangia, indicating that the beetle must supply nutrients and growth factors (Norris, 1979).

The plant-pathogenic *Ophiostoma* apparently are vectored non-specifically on the exterior of the adult beetle or, in the case of *D. frontalis*, by two species of phoretic mites in the genus *Tarsonemus*. These mites carry ascospores of *O. minus* in a special spore-carrying structure called a sporotheca (Moser, 1985). *Tarsonemus* were common in *D. frontalis* infestations where *O. minus* was abundant; conversely, significantly fewer *Tarsonemus* were seen in infestations where the pathogen was rare (Bridges and Moser, 1986).

Bark beetles benefit from their fungal mutualists in many ways. Some examples are reviewed here with respect to the similarities and differences among different fungus/bark beetle associations.

7.2.6.1 Death of the host tree

Inoculation experiments have demonstrated that *Ophiostoma* spp. can colonize extensively and kill their hosts (Basham, 1970; Owen *et al.*, 1987). Therefore, these fungi are presumed to be responsible for host death. However, tree mortality often occurs so rapidly that there is some question whether these fungi are solely responsible (Whitney and Cobb, 1972; Parmeter *et al.*, 1989). In several cases, the extent of colonization and penetration by *Ophiostoma* has been limited before and even after the host trees have died. This has been observed for *Pinus taeda* killed in *D. frontalis* infestations (Bridges *et al.*, 1985) and for *P. ponderosa* killed in *D. brevicomis* infestations (Whitney, 1982; Whitney and Cobb, 1972).

These observations suggest that factors other than extensive colonization may be important in causing mortality, for example, production of systemic toxins by the pathogens (Hemingway *et al.*, 1977; Chapter 8). Detailed investigations of the host–fungal pathogen interactions are needed to clarify the role(s) of these fungi and/or their metabolites in tree mortality.

Most other mutualistic fungi apparently are not involved in the death of the host tissues, a requirement for successful larval development and ultimately for beetle reproduction. Deep penetration by these mutualistic fungi into the sapwood has not been demonstrated. Rapid and deep invasion would be required to disrupt host water conduction, leading to death of the tree.

7.2.6.2 Requirement for gallery production

Most research has shown that mutualistic fungi carried in the mycangia of female beetles during initial attack on a suitable host are not important to egg-gallery mining and egg laying. Barras (1973) showed that the length of galleries and number of eggs per gallery length did not differ between *D. frontalis* that had or lacked mycangial fungi. Recently, however, work with both parent and progeny generations of *D. frontalis* by Goldhammer *et al.* (1990) indicated that mining and egg laying were decreased in the absence of mycangial fungi.

7.2.6.3 Conditioning of host tissues for brood development

Research with *D. frontalis*, in particular, has shown clearly that mycangial fungi improve larval mining, duration of brood development, survival of larvae to adults, and adult beetle size (Barras, 1970; Bridges, 1985; Bridges and Perry, 1985; Goldhammer *et al.*, 1990). The mechanism(s) by which these fungi affect reproductive parameters is not clear. The mycangial fungi are found along the egg galleries and larval mines, and in the pupal chambers where they presumably infest the newly emerging brood adults. The timing of fungal growth and development in relation to changes in host tissues during larval development have not been clearly defined.

By contrast, the importance of mycangial fungi and mutualistic yeasts in preparing *Pinus contorta* phloem for *D. ponderosae* larval mining is questionable. Whitney (1971) has shown that newly laid eggs are deposited and second-to-fourth instar larvae mine in phloem that lacks mutualistic fungi and yeasts. Mining and pupation occurred several millimeters ahead of the growing fungi in essentially axenic non-discolored phloem. The fungi eventually colonize the pupal chambers and reinfest the new brood adults.

7.2.6.4 Mutualistic fungi as a food source

The ambrosial growth habit of some mutualistic fungi within the galleries, mines and pupal chambers of conifer bark beetles has been interpreted to indicate their use as a food source for brood development. However, there is little evidence that fungivory is required by conifer bark beetles. Several non-aggregating *Dendroctonus* species (*D. micans, D. punctatus, D. terebrans* and *D. valens*) have no known fungal mutualists and feed on unaltered host tissues (Berryman, 1989). Some species can be raised *in vitro* on sterile phloem or wood bolts and show no requirement for specific fungi; however, yeast extract can enhance beetle development and survival *in vitro* (Bedard, 1966; Strongman, 1987).

In the mutualistic association between *D. ponderosae* and *O. montium*, *O. clavigerum* and yeasts, the second-to-fourth instar larvae mine phloem in advance of these fungi

(Whitney, 1971). This would preclude these fungi as a food source for the larvae. Observations on the development of pupae and teneral adults, however, suggested that consumption of these fungi occurred during the final stages of brood development.

7.2.6.5 Interactions between fungal mutualists and Ophiostoma

Observations and experiments have suggested that factors within tissues colonized by *Ophiostoma* are detrimental to beetle brood development. Larvae mine away from tissues colonized by *Ophiostoma* and expend more energy in producing longer, winding galleries (Barras, 1970; Franklin, 1970; Yearian *et al.*, 1972). Female *D. frontalis* forced to mine and oviposit in *Ophiostoma*-infected tissues produced smaller broods with extended development times (Barras, 1970; Paine and Stephen, 1988). Other observations and a few experiments have shown that the mutualistic fungi may benefit the beetles by restricting the development of *Ophiostoma*. In southern pines and *P. ponderosa*, *Ophiostoma* spp. often are restricted in their invasion to sectors in the sapwood and associated phloem, while surrounding tissues are colonized heavily by the mutualistic fungi (Barras, 1970; Whitney and Cobb, 1972). In experimental work, *Ophiostoma* was restricted in pine bolts infested by *D. frontalis* carrying their mycangial fungi but was more extensive in tissues infested by female beetles deprived of mycangial fungi (Bridges and Perry, 1985). How the mycangial fungi restrict growth of *Ophiostoma* is unknown. Perhaps they out-compete the *Ophiostoma* for specific nutrients, but antibiosis does not appear to be involved. Differences in inoculum loads between *Ophiostoma* and mycangial mutualists may influence the initiation and speed of *D. frontalis* infestation growth.

7.2.6.6 Production of pheromones

Mutualistic fungi, yeasts and bacteria associated with conifer bark beetles have been shown to convert host tree terpenes into beetle aggregation pheromones (Chapter 6). Mutualistic symbionts also can produce various volatile products including alcohols that augment the effectiveness of the beetle pheromones. With *D ponderosae*, the mutualistic fungi can oxidize the aggregation pheromone *trans*-verbenol to the anti-aggregation pheromone verbenone and thus may signal the termination of a successful mass attack (Borden *et al.*, 1986).

7.2.7 Natural enemies of associates

Many families and genera that are commonly reared from bark beetle-infested material (Table 7.1) are thought to be predaceous or parasitic on other associated species found with bark beetles. The Platygasteridae, for example, probably are parasitoids of the many fungus-feeding larvae of the dipteran families Sciaridae or Cecidomyiidae found at the phloem–sapwood interface in bark beetle-infested trees. Not only are insect natural enemies encountered, but the variety of mites, pseudoscorpions, and other arachnids that are predaceous on some of the associated community is vast. Unfortunately the biology and role of most are relatively unknown.

7.2.8 Tree decomposers

Large saprophages such as the Cerambycidae and Buprestidae function as wood degraders. These species feed on decomposing tissue and also vector wood-decomposing fungi that grow in this habitat. Exclusion of these insects from logs can slow decomposition significantly (Edmonds and Eglitis, 1989).

Various saprophytic invertebrates and spores of non-vectored fungi find easier access to decaying tissues under the bark following penetration by bark beetles and other wood boring insects (Käärik, 1974; Schowalter *et al.*, 1992). Pathogenic fungi often persist as saprophytes in the decaying tree. *Ophiostoma* spp., other ascomycetes and deuteromycetes, and some bacteria degrade cell contents and cause "soft rot"; *Heterobasidion annosum*, *Armillaria* spp., and other basidiomycete "decay" fungi are capable of enzymatic degradation of cellulose and/or lignin (Käärik, 1974; Rayner and Todd, 1979). Initial colonization by soft rot organisms can inhibit decay fungi through antibiosis and resource depletion or, with nitrogen-fixing bacteria, can stimulate decay fungi through provision of necessary nitrogen, vitamins and other resources and degradation of toxic substances (Käärik, 1974; Blanchette and Shaw, 1978; Barz and Weltring, 1985).

These organisms ultimately are responsible for the decomposition and mineralization of wood and cycling of nutrients from dead trees. Roots and mycorrhizal fungi infuse decaying logs and transport nutrients into living plants. Schowalter *et al.* (1992) provide more detailed discussion and current literature on this topic.

7.3 ARRIVAL SEQUENCE

Stephen and Dahlsten (1976a) noted two basic arrival/colonization patterns for *D. brevicomis* in *P. ponderosa*. The first pattern, exemplified in Fig. 7.5, reflects rapid mass attack during the first summer flight period when synchronized emergence of overwintering beetles results in large populations of adults available for colonization. A slower, more extended attack period was found during the second generation of *D. brevicomis*, when populations of adults are less dense due to lack of synchronization in emergence (Fig. 7.6). The type of arrival pattern exhibited in Fig. 7.5 also would be expected for bark beetle species, such as *D. frontalis* and *D. ponderosae* that require large population sizes to respond rapidly and overcome tree resistance (McCambridge, 1967; Gara and Coster, 1968; Dixon and Payne, 1979). Ashraf and Berryman (1969) found a somewhat slower, more extended colonization period with *Scolytus ventralis* in *Abies grandis*. Berisford and Franklin (1971) noted a rapid arrival pattern with *I. avulsus* (Fig. 7.5). *Ips grandicollis*, normally seen attacking weak hosts or slash, shows a different pattern of gradual arrival (Fig. 7.6). The amplitude and periodicity of the arrival curves for other bark beetles likely reflect temperatures, beetle population density, and the importance of mass arrival for successful colonization of a temporary resource.

In addition to the primary species that may be responsible for tree death, there are many secondary bark and ambrosia beetles that respond rapidly to the newly created habitat in the dead or dying tree. Many of these species respond to primary (plant-produced) or secondary (insect-produced) attractants during host selection and concentration (Borden, 1982). The role of microorganisms in attraction was proposed by Person (1931), subsequently discounted (Graham, 1967), and recently reconsidered (Borden, 1982; Dahlsten and Berisford, unpublished). Interspecific communication among bark beetle species that inhabit the same host has been established (Birch and Wood, 1975) and is important in the interactions among these species (Borden, 1982; Lewis and Cane, 1990).

Response of bark beetle predators and parasitoids to bark beetle aggregation pheromones was first demonstrated by Wood *et al.* (1968) and Bedard (1966), respectively. Since that

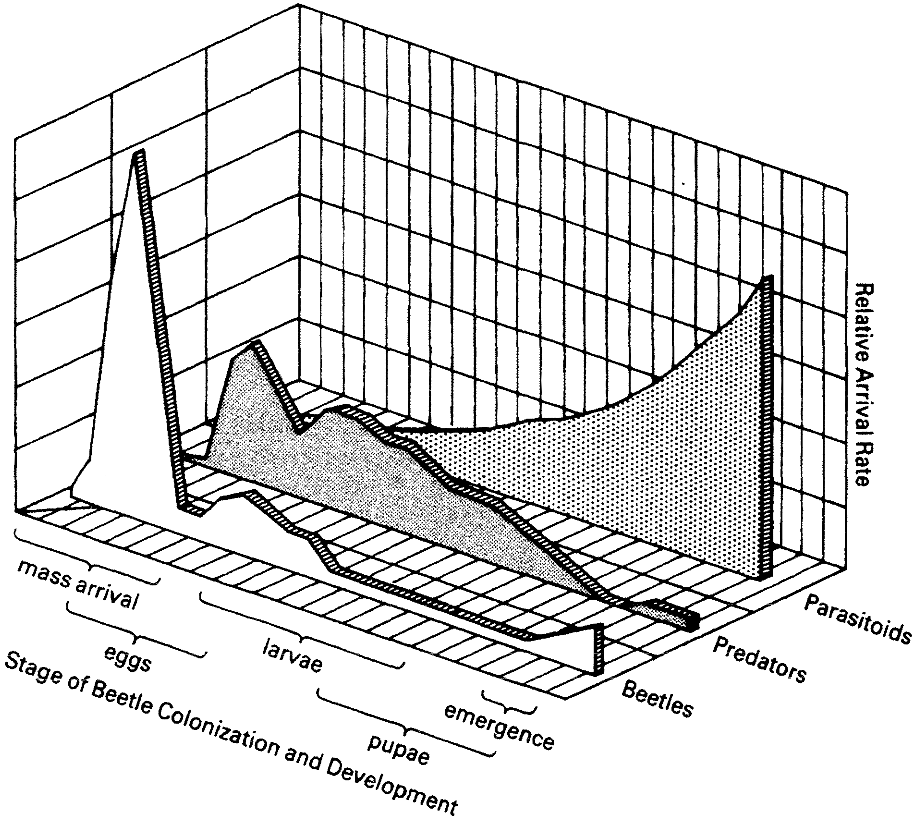


Fig. 7.5. Generalized pattern of primary bark beetle, predator and parasitoid arrival in relation to stage of the beetles' colonization and within-tree development.

time, many natural enemies now have been shown to respond to a wide variety of beetle and host-produced compounds. Payne (1989) provides examples of 29 species, from four insect orders, of natural enemies that rely on bark beetle-associated olfactory stimuli for host location.

The complex of natural enemies and other arthropod associates of conifer-infesting bark beetles arrives at its host tree in a predictable sequence that has been described in detail for at least two species of *Dendroctonus, D. brevicomis* (Stephen and Dahlsten, 1976b) and *D. frontalis* (Camors and Payne, 1973; Dixon and Payne, 1979), for *Ips* species (Berisford and Franklin, 1971; Berisford, 1974), and for *S. ventralis* (Ashraf and Berryman, 1969). Chemicals produced by these beetles, the host tree, and fungi interact to influence the predictable arrival of associated arthropods selecting suitable host locations. The sequence of arrival that has been observed for these bark beetles and their associates can be generalized as follows.

The arrival patterns of natural enemies and other associates is consistent for particular guilds (Stephen and Dahlsten, 1976b). Generalized patterns for guilds of natural enemies and other associates are proposed in Figs 7.5 and 7.6. Predators, primarily those that feed on attacking adult bark beetles, respond during and shortly after mass attack. In some species a second peak in predator response, perhaps associated with re-emerging parent adult bark beetles, has been observed. A more gradual arrival pattern is seen with the generalist preda-

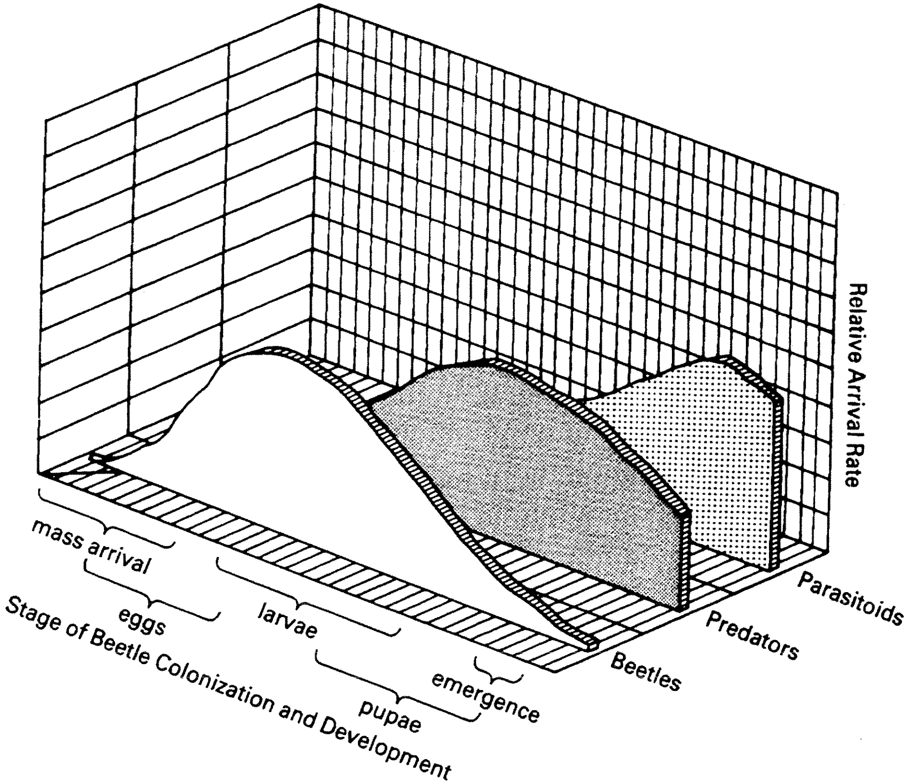


Fig. 7.6. Generalized arrival pattern for bark beetles, predators and parasitoids of less aggressive bark beetle species and those whose population densities are sufficiently low as to require a protracted period of mass arrival for successful colonization

tors, wood decomposers and fungivores. Bark beetle parasitoids, that must arrive when suitable stages of immature beetles are present, show a rapidly increasing response later in the beetle life cycle. The constancy of these overall patterns is seen for different parasitoid species with similar host requirements (Fig. 7.7) and for numerous groups of other arthropod associates sharing similar host requirements.

Recent research indicates the potential importance of a third trophic level interaction. Microorganisms play a role in producing chemicals to which parasites and perhaps other associates can respond. Most members of the parasitoid guilds of both *D. frontalis* and *D. brevicomis* are strongly attracted to billets infected with fungi and/or yeasts from these beetles (Dahlsten and Berisford, unpublished).

7.4 IMPACT OF NATURAL ENEMIES

Many species have been identified as natural enemies of the primary colonizers and the influence of these associates in natural control of bark beetle populations has been debated. With some exceptions (e.g. Hain and McClelland, 1979; Amman, 1984) most populations of bark beetles have been studied during outbreaks. In those situations it appeared that natural enemies had not been successful in preventing the outbreak. Natural enemies frequently are ascribed an important role at endemic, or low, population levels, but are credited

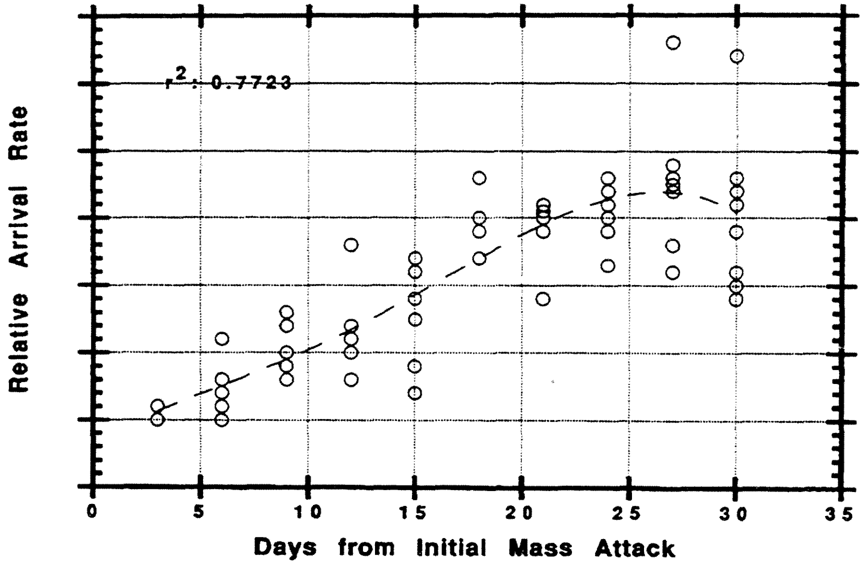


Fig. 7.7. Generalized arrival rate for eight species of *D. frontalis* parasitoids. (Data from Dixon and Payne, 1979.)

with minimal impact once bark beetle populations reach epidemic population levels. Unfortunately, little research has been designed to ascertain their actual importance. The literature on impact of arthropod parasitoids and predators on bark beetle population dynamics is scarce, and recent reviews by Berisford (1980), Dahlsten (1982), Mills (1983), Moeck and Safranyik (1984), and an edited book on the potential for biological control (Kulhavy and Miller, 1989) reveal little substantiative information to clarify their role.

Numerous authors have measured bark beetle mortality caused by individual species or complexes of natural enemies (see Dahlsten, 1982). Within-tree mortality caused by insect predators, parasitic mites, nematodes and insects averaged 17% in combined life tables for *S. ventralis* in *Abies grandis* (Berryman and Ferrell, 1988). Linit and Stephen (1983) and Moore (1972) reported about 25% within-tree mortality attributable to natural enemies of *D. frontalis*. Amman (1984) estimated that insect parasites and predators killed 8%, 33%, and 4% of *D. ponderosae* within trees in endemic, epidemic and postepidemic infestations, respectively.

Data from Stephen *et al.* (1989) revealed increased within-tree mortality from natural enemies of *D. frontalis* during the progression from endemic to epidemic to postepidemic population phases. Amman (1984) and Cole (1981), however, did not see similar responses with *D. ponderosae* populations. Recently Turchin (1990) and Turchin *et al.* (1991) have analyzed long-term population indices of *D. frontalis* abundance statistically and concluded that delayed density-dependent processes are responsible for regulating *D. frontalis* populations. They propose that natural enemies may provide this regulation. The variation in mortality and its relationship to host density must be understood if the role of natural enemies is to be evaluated properly.

Research to evaluate the importance of natural enemies in the dynamics of bark beetle populations should be designed to determine the extent to which natural enemy populations exhibit density dependent responses to their bark beetle host. This could be accomplished by measuring the absolute population densities of the bark beetle and its natural enemies over time. This seems a simple task in concept, but the effort needed to provide adequate estimations of populations of all the organisms involved is expensive and difficult. Adequate sampling protocols have been studied in depth for some bark beetles species, but not for others. However, adequate sampling techniques for estimation of natural enemy populations rarely have been considered, particularly in relationship to the host beetle populations involved. Stephen and Taha (1976) found that within-tree populations of parasitoids and predators were more highly aggregated than *D. frontalis*. Thus, accurate estimation of natural enemy density required larger sample units and sample size than did bark beetle life stages.

7.5 CONCLUSIONS

An extensive complex of organisms, primarily arthropods and fungi, rapidly colonize trees that are attacked and killed by bark beetles and pathogenic fungi. The composition and arrival sequence of this community are predictable in space and time, and appear similar in terms of community dynamics among bark beetle–conifer associations. Interactions among key elements in this complex, arthropod natural enemies and mutualistic fungi, can affect reproduction and survival of bark beetles and pathogenic fungi significantly. However, these interactions have not been studied in sufficient detail to assess their role in regulating bark beetle or pathogen epidemiologies.

REFERENCES

Amman, G.D. (1984). Mountain pine beetle (Coleoptera: Scolytidae) mortality in three types of infestations. *Environ. Entomol.* **13**, 184–191.

Ashraf, M. and Berryman, A.A. (1969). Biology of *Scolytus ventralis* (Coleoptera: Scolytidae) attacking *Abies grandis* in northern Idaho. *Melanderia* **2**, 1–23.

Barras, S.J. (1970). Antagonism between *Dendroctonus frontalis* and the fungus *Ceratocystis minor*. *Ann. Entomol. Soc. Am.* **63**, 1187–1190.

Barras, S.J. (1973). Reduction of progeny and development in the southern pine beetle following removal of symbiotic fungi. *Can. Entomol.* **105**, 1295–1299.

Barz, W. and Weltring, K.-M. (1985). Biodegradation of aromatic extractives of wood. *In* "Biosynthesis and Biodegradation of Wood Components" (T. Higuchi, ed.), pp. 607–666. Academic Press, Orlando, FL.

Basham, H.G. (1970). Wilt of loblolly pine inoculated with blue-stain fungi of the genus *Ceratocystis*. *Phytopathology* **60**, 750–754.

Batra, L.R., ed. (1979). "Insect–Fungus Symbiosis: Nutrition, Mutualism, and Commensalism". Allanheld, Osmund & Co., Montclair, NJ, 276 pp.

Beaver, R.A. (1989). Insect–fungus relationships in the bark and ambrosia beetles. *In* "Insect–Fungus Interactions" (N. Wilding, N.M. Collins, P.M. Hammond and J.F. Webber, eds), pp. 121–143. Academic Press, London.

Bedard, W.D. (1966). A ground phloem medium for rearing immature bark beetles (Scolytidae). *Ann. Entomol. Soc. Am.* **59**, 931–938.

Berisford, C.W. (1974). Parasite abundance in *Ips* spp. infestations as influenced by the southern pine beetle. *Environ. Entomol.* **3**, 695–696.

Berisford, C.W. (1980). Natural enemies and associated organisms. *In* "The Southern Pine Beetle" (R.C. Thatcher, J.L. Searcy, J.E. Coster and G.D. Hertel, eds), pp. 31–52. USDA Forest Serv. Tech. Bull. 1631, Washington, DC.

Berisford, C.W. and Franklin, R.T. (1971). Attack patterns of *Ips avulsus* and *I. grandicollis* (Coleoptera: Scolytidae) on four species of southern pines. *Ann. Entomol. Soc. Am.* **64**, 894–897.

Berryman, A.A. (1989). Adaptive pathways in scolytid–fungus associations. *In* "Insect–Fungus Interactions" (N. Wilding, N.M. Collins, P.M. Hammond and J.F. Webber, eds), pp. 145–159. Academic Press, London.

Berryman, A.A. and Ferrell, G.T. (1988). The fir engraver beetle in western states. *In* "Dynamics of Forest Insect Populations: Patterns, Causes, Implications" (A.A. Berryman, ed.), pp. 555–577. Plenum Press, New York.

Birch, M.C. and Wood, D.L. (1975). Mutual inhibition of the attractant pheromone reponse by two species of *Ips* (Coleoptera: Scolytidae). *J. Chem. Ecol.* **1**, 101–113.

Birch, M.C., Svihra, P. and Miller, J.C. (1980). Influence of chemically medicated behaviour on host tree colonization by four cohabiting species of bark beetles. *J. Chem. Ecol.* **6**, 395–414.

Blackman, M.W. and Stage, H.H. (1924). On the succession of insects living in the bark and wood of dying, dead and decaying hickory. *In* NY State College of Forestry Tech. Publ. 17, pp. 3–268. Syrecuse, NY.

Blanchette, R.A. and Shaw, C.G. (1978). Associations among bacteria, yeasts, and basidiomycetes during wood decay. *Phytopathology* **68**, 631–637.

Borden, J.H. (1982). Aggregation pheromones. *In* "Bark Beetles in North American Conifers" (J.B. Mitton and K.B. Sturgeon, eds), pp. 74–139. University of Texas Press, Austin, TX.

Borden, J.H., Hunt, D.W.A., Miller, D.R. and Slessor, K.N. (1986). Orientation in forest Coleoptera: an uncertain outcome to responses by individual beetles to variable stimuli. *In* "Mechanisms in Insect Olfaction" (T.L. Payne, M.C. Birch and C.E.J. Kennedy, eds), pp. 97–109. Oxford University Press, Oxford.

Bridges, J.R. (1985). Relationship of symbiotic fungi to southern pine beetle population trends. *In* "Integrated Pest Management Research Symposium: the Proceedings" (S.J. Branham and R.C. Thatcher, eds), pp. 127–135. USDA Forest Serv. Gen. Tech. Rpt. SO-56. USDA Forest Serv., Southern Forest Exp. Stn., New Orleans, LA.

Bridges, J.R. and Moser, J.C. (1986). Relationship of phoretic mites (Acari: Tarsonemidae) to the bluestaining fungus, *Ceratocystis minor*, in trees infested by southern pine beetle (Coleoptera: Scolytidae). *Environ. Entomol.* **15**, 951–953.

Bridges, J.R. and Perry, T.J. (1985). Effects of mycangial fungi on gallery construction and distribution of blue-stain in southern pine beetle infested pine bolts. *J. Entomol. Sci.* **20**, 271–275.

Bridges, J.R., Nettleton, W.A. and Conner, M.D. (1985). Southern pine beetle (Coleoptera: Scolytidae) infestations without the bluestain fungus, *Ceratocystis minor*. *J. Econ. Entomol.* **78**, 325–327.

Camors, F.B., Jr. and Payne, T.L. (1973). Sequence of arrival of entomophagous insects to trees infested with the southern pine beetle. *Environ. Entomol.* **2**, 267–270.

Cole, W.E. (1981). Some risks and causes of mortality in mountain pine beetle populations: a long-term analysis. *Res. Popul. Ecol.* **23**, 116–144.

Coulson, R.N., Pope, D.N., Gagne, J.A., Fargo, W.S., Pulley, P.E., Edson, L.J. and Wagner, T.L. (1980). Impact of foraging by *Monochamus titillator* (Col.: Cerambycidae) on within-tree populations of *Dendroctonus frontalis* (Col.: Scolytidae). *Entomophaga* **25**, 155–170.

Cross, E.A., Moser, J.C. and Rack, G. (1981). Some new forms of *Pyemotes* (Acarina: Pyemotidae) from forest insects with remarks on polymorphism. *Int. J. Acarol.* **7**, 179–196.

Dahlsten, D.L. (1982). Relationships between bark beetles and their natural enemies. *In* "Bark Beetles in North American Conifers" (J.B. Mitton and K.B. Sturgeon, eds), pp. 140–182. University of Texas Press, Austin, TX.

Dixon, W.N. and Payne, T.L. (1979). Sequence of arrival and spatial distribution of entomophagous and associate insects on southern pine beetle-infested trees. Texas A&M University Agric. Exp. Stn. Bull. MP-1432, College Station, TX.

Edmonds, R.L. and Eglitis, A. (1989). The role of the Douglas-fir beetle and wood borers in the decomposition and nutrient release from Douglas-fir logs. *Can. J. For. Res.* **19**, 853–859.

Espelie, K.E., Berisford, C.W. and Dahlsten, D.L. (1990). Cuticular hydrocarbons of geographically isolated populations of *Rhopalicus pulchripennis* (Hymenoptera: Pteromalidae): evidence for two species. *Comp. Biochem. Physiol.* **968**, 305–308.

Flamm, R.O., Wagner, T.L., Cook, S.P., Pulley, P.E., Coulson, R.N. and McArdle, T.M. (1987). Host colonization by cohabiting *Dendroctonus frontalis*, *Ips avulsus*, and *I. calligraphus* (Coleoptera: Scolytidae). *Environ. Entomol.* **16**, 390–399.

Flamm, R.O., Coulson, R.N., Beckley, P., Pulley, P.E. and Wagner, T.L. (1989). Maintenance of a phloem-inhabiting guild. *Environ. Entomol.* **18**, 381–387.

Franklin, R.T. (1970). Observations on the blue stain–southern pine beetle relationship. *J. Georgia Entomol. Soc.* **5**, 53–57.

Gara, R.I. and Coster, J.E. (1968). Studies on the attack behavior of the southern pine beetle. III. Sequence of tree infestation within stands. *Contrib. Boyce Thompson Inst.* **24**, 77–85.

Goldfarb, B., Nelson, E.E. and Hansen, E.M. (1989) *Trichoderma* species from Douglas-fir stumps and roots infested with *Phellinus weirii* in the western Cascade Mountains of Oregon. *Mycologia* **81**, 134–138.

Goldhammer, D.S., Stephen, F.M. and Paine, T.D. (1990). The effect of the fungi *Ceratocystis minor* (Hedgecock) Hunt, *Ceratocystis minor* (Hedgecock) Hunt var. *barrasii* Taylor, and SJB 122 on reproduction of the southern pine beetle, *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae). *Can. Entomol.* **122**, 407–418.

Graham, K. (1967). Fungal–insect mutualism in trees and timber. *Annu. Rev. Entomol.* **12**, 105–126.

Hain, F.P. and McClelland, W.T. (1979). Studies of declining and low level populations of the southern pine beetle in North Carolina. *In* "Proceedings of the Population Dynamics of Forest Insects at Low Levels" (F.P. Hain, ed.), pp. 9–26. North Carolina State Univ., Raleigh, NC.

Hemingway, R.W., McGraw, G.W. and Barras, S.J. (1977). Polyphenols in *Ceratocystis minor* -infected *Pinus taeda*: fungal metabolites, phloem and xylem phenols. *J. Agric. Food Chem.* **25**, 717–720.

Hoffard, W.H. and Coster, J.E. (1976). Endoparasitic nematodes of *Ips* bark beetles in Eastern Texas. *Environ. Entomol.* **5**, 128–132.

Hunter, P.E., Rosario, R.M.T. and Moser, J.C. (1989). Two new species of *Ereynetes* (Acari: Prostigmata: Ereynetidae) associated with bark beetles. *J. Entomol. Sci.* **24**, 16–20.

Käärik, A.A. (1974). Decomposition of wood. *In* "Biology of Plant Litter Decomposition" (C.H. Dickinson and G.J. F. Pugh, eds), pp. 129–174. Academic Press, London.

Kinn, D.N. (1971). The life cycle and behavior of *Cercoleipus coelonotus* (Acarina: Mesostigmata). Univ. Calif. Publ. Entomol. 65, 1–66. University of California Press, Berkeley, CA.

Kinn, D.N. (1980). Mutualism between *Dendrolaelaps neodisetus* and *Dendroctonus frontalis*. *Environ. Entomol.* **9**, 756–758.

Kinn, D.N. and Linit, M.J. (1989). A key to phoretic mites commonly found on long-horned beetles emerging from southern pines. USDA Forest Serv. Res. Note S0-357, USDA Forest Serv., Southern Forest Exp. Stn., New Orleans, LA, 8 pp.

Kinn, D.N. and Witcosky, J.J. (1978). The life cycle and behavior of *Macrocheles boudreauxi* Krantz. *Z. Ang. Entomol.* **84**, 136–144.

Kulhavy, D.L. and Miller, M.C. (1989). "Potential for Biological Control of *Dendroctonus* and *Ips* Bark Beetles." Stephen F. Austin State University Press, Nacogdoches, TX, 255 pp.

Lanier, G.N., Hendrichs, J.P. and Flores, J.E. (1988). Biosystematics of the *Dendroctonus frontalis* (Coleoptera: Scolytidae) complex. *Ann. Entomol. Soc. Am.* **81**, 403–418.

Lewis, E.E. and Cane, J.H. (1990). Pheromonal specificity of southeastern *Ips* pine bark beetles reflects phylogenetic divergence (Coleoptera: Scolytidae). *Can. Entomol.* **12**, 1235–1238.

Lindquist, E.E. (1969). Review of Holarctic tarsonemid mites (Acarina: Prostigmata) parasitizing eggs of Ipine bark beetles. *Mem. Entomol. Soc. Can.* **60**, 1–111.

Linit, M.J. and Stephen, F.M. (1983). Parasite and predator component of within-tree southern pine beetle (Coleoptera: Scolytidae) mortality. *Can. Entomol.* **115**, 679–688.

Massey, C.L. (1974). Biology and taxonomy of nematode parasites and associates of bark beetles in the United States. USDA Forest Serv. Agric. Handbook 446. USDA Forest Serv., Washington, DC, 233 pp.

McCambridge, W.F. (1967). Nature of induced attacks by the Black Hills beetle, *Dendroctonus ponderosae* (Coleoptera: Scolytidae). *Ann. Entomol. Soc. Am.* **60**, 920–928.

Miller, M.C. (1985). The effect of *Monochamus titillator* (F.)(Col., Cerambycidae) foraging on the emergence of *Ips calligraphus* (Germ.) (Coleoptera: Scolytidae) insect associates. *Z. Ang. Entomol.* **100**, 189–197.

Mills, N.J. (1983). The natural enemies of scolytids infesting conifer bark in Europe in relation to the biological control of *Dendroctonus* spp. in Canada. CIBC Biocontrol News Info. **4**, 305–328.

Moeck, H.A. and Safranyik, L. (1984). Assessment of predator and parasitoid control of bark beetles. Canadian Forestry Serv. Info. Rept. BC-X-248. Pacific Forest Research Centre, Victoria, BC.

Moore, G.E. (1971). Mortality factors caused by pathogenic bacteria and fungi of the southern pine beetle in North Carolina. *J. Invert. Pathol.* **17**, 28–37.

Moore, G.E. (1972). Southern pine beetle mortality in North Carolina caused by parasites and predators. *Environ. Entomol.* **1**, 58–65.

Moser, J.C. (1975). Mite predators of the southern pine beetle. *Ann. Entomol. Soc. Am.* **68**, 1113–1116.

Moser, J.C. (1976). Surveying mites (Acarina) phoretic on the southern pine beetle (Coleoptera: Scolytidae) with sticky traps. *Can. Entomol.* **108**, 809–813.

Moser, J.C. (1981). Transfer of a *Pyemotes* egg parasite phoretic on western pine bark beetles to the southern pine beetle. *Int. J. Acarol.* **7**, 197–202.

Moser, J.C. (1985). Use of sporothecae by phoretic *Tarsonemus* mites to transport ascospores of coniferous bluestain fungi. *Trans. Br. Mycol. Soc.* **84**, 750–753.

Moser, J.C. and Roton, L.M. (1971). Mites associated with southern pine bark beetles in Allen Parish, Louisiana. *Can. Entomol.* **103**, 1775–1798.

Moser, J.C., Cross, E.A. and Roton, L.M. (1971). Biology of *Pyemotes parviscolyti* (Acarina: Pyemotidae). *Entomophaga* **16**, 367–379.

Norris, D.M. (1979). The mutualistic fungi of Xyleborini beetles. *In* "Insect–Fungus Symbiosis: Nutrition, Mutualism and Commensalism" (L.R. Batra, ed.), pp. 53–63. Allanheld, Osmun & Co., Montclair, NJ.

Owen, D.R., Lindahl, K.Q., Jr., Wood, D.L. and Parmeter, J.R., Jr. (1987). Pathogenicity of fungi isolated from *Dendroctonus valens*, *D. brevicomis*, and *D. ponderosae* to ponderosa pine seedlings. *Phytopathology* **77**, 631–636.

Paine, T.D. and Stephen, F.M. (1988). Induced defenses of loblolly pine, *Pinus taeda*: potential impact on *Dendroctonus frontalis* within-tree mortality. *Entomol. Exp. Appl.* **46**, 39–46.

Paine, T.D., Birch, M.C. and Svihra, P. (1981). Niche breadth and resource partitioning by four sympatric species of bark beetles (Coleoptera: Scolytidae). *Oecologia* **48**, 1–6.

Parmeter, J.R., Slaughter, G.W., Chen, M., Wood, D.L. and Stubbs, H.A. (1989). Single and mixed inoculations of ponderosa pine with fungal associates of *Dendroctonus* spp. *Phytopathology* **79**, 768–772.

Payne, T.L. (1989). Olfactory basis for insect enemies of allied species. *In* "Potential for Biological Control of *Dendroctonus* and *Ips* Bark Beetles" (D.L. Kulhavy and M.C. Miller, eds), pp. 55–69. Stephen F. Austin State University Press, Nacogdoches, TX.

Person, H.L. (1931). Theory in explanation of the selection of certain trees by the western pine beetle. *J. Forestry* **31**, 696–699.

Rayner, A.D.M. and Todd, N.K. (1979). Population and community structure and dynamics of fungi in decaying wood. *Adv. Bot. Res.* **7**, 333–420.

Savely, H.E. (1939). Ecological relations of certain animals in dead pine and oak logs. *Ecol. Monogr.* **9**, 321–385.

Schowalter, T.D., Caldwell, B.A., Carpenter, S.E., Griffiths, R.P., Harmon, M.E., Ingham, E.R., Kelsey, R.G., Lattin, J.D. and Moldenke, A.R. (1992). Decomposition of fallen trees: effects of initial conditions and heterotroph colonization rates. *In* "Tropical Ecosystems: Ecology and Management" (K.P. Singh and J.S. Singh, eds), pp. 373–383. Wiley Eastern Ltd., New Delhi.

Shelford, V.E. (1913). Animal communities in temperate America. *Bull. Geo. Soc. Chicago* **5**, 362.

Sikorowski, P.P., Pabst, G.S. and Tomson, O. (1979). "The impact of diseases on southern pine beetle in Mississippi." Mississippi State Agric. Exp. Stn. Tech. Bull. 99. Mississippi State, MS. 9 pp.

Stephen, F.M. and Dahlsten, D.L. (1976a). The temporal and spatial arrival pattern of *Dendroctonus brevicomis* Le Conte in ponderosa pine. *Can. Entomol.* **108**, 271–282.

Stephen, F.M. and Dahlsten, D.L. (1976b). The arrival sequence of the arthropod complex following attack by *Dendroctonus brevicomis* (Coleoptera: Scolytidae) in ponderosa pine. *Can. Entomol.* **108**, 283–304.

Stephen, F.M. and Taha, H.A. (1976). Optimization of sampling effort for within-tree-populations of southern pine beetle and its natural enemies. *Environ. Entomol.* **5**, 1001–1007.

Stephen, F.M., Lih, M.P. and Wallis, G.W. (1989). Impact of arthropod natural enemies on *Dendroctonus frontalis* (Coleoptera: Scolytidae) mortality and their potential role in infestation growth. *In* "Biological Control of *Dendroctonus* and *Ips* Bark Beetles" (D.L. Kulhavy and M.C. Miller, eds), pp. 169–185. Stephen F. Austin State University Press, Nacogdoches, TX.

Strongman, D.B. (1987). A method for rearing *Dendroctonus ponderosae* Hopk. (Coleoptera: Scolytidae) from eggs to pupae on host tissue with or without a fungal complement. *Can. Entomol.* **119**, 207–208.

Thong, C.H.S. and Webster J.M. (1975). Effects of the bark beetle nematode, *Contortylenchus reversus*, on gallery construction, fecundity, and egg viability of the Douglas-fir beetle *Dendroctonus pseudotsugae* (Coleoptera: Scolytidae). *J. Invert. Pathol.* **26**, 235–238.

Turchin, P. (1990). Rarity of density dependence or population regulation with lags? *Nature* **344**, 660–663.

Turchin, P., Lorio, P.L., Jr., Taylor, A.D. and Billings, R.F. (1991). Why do populations of southern pine beetles (Coleoptera: Scolytidae) fluctuate? *Environ. Entomol.* **20**, 401–409.

Wagner, T.L., Flamm, R.O. and Coulson, R.N. (1985). Strategies for cohabitation among the southern pine bark beetle species: comparisons of life-process biologies. *In* "Integrated Pest Management Research Symposium: the Proceedings" (S.J. Branham and R.C. Thatcher, eds) pp. 87–101. USDA Forest Serv. Gen. Tech. Rpt. SO-56, USDA Forest Serv., Southern Forest Exp. Stn., New Orleans, LA.

Webber, J.F. and Gibbs, J.N. (1989). Insect dissemination of fungal pathogens of trees. *In* "Insect–Fungus Interactions" (N. Wilding, N.M. Collins, P.M. Hammond and J.F. Webber, eds), pp. 161–193. Academic Press, London.

Whitney, H.S. (1971). Association of *Dendroctonus ponderosae* (Coleoptera: Scolytidae) with blue stain fungi and yeasts during brood development in lodgepole pine. *Can. Entomol.* **103**, 1495–1503.

Whitney, H.S. (1982). Relationships between bark beetles and symbiotic organisms. *In* "Bark Beetles in North American Conifers" (J.B. Mitton and K.B. Sturgeon, eds), pp. 183–211. University of Texas Press, Austin, TX.

Whitney, H.S. and Cobb, F.W., Jr. (1972). Non-staining fungi associated with the bark beetle *Dendroctonus brevicomis* (Coleoptera: Scolytidae) on *Pinus ponderosa*. *Can. J. Bot.* **50**, 1943–1945.

Wilson, D.S. (1980). "The Natural Selection of Populations and Communities". Benjamin/Cummings Publishing Co., Inc., Menlo Park, CA. 186 pp.

Witcosky, J.J., Schowalter, T.D. and Hansen, E.M. (1986). *Hylastes nigrinus* (Coleoptera: Scolytidae), *Pissodes fasciatus* and *Steremnius carinatus* (Coleoptera: Curculionidae) as vectors of black-stain root disease of Douglas-fir. *Environ. Entomol.* **15**, 1090–1095.

Wood, D.L., Browne, L.E., Bedard, W.D., Tilden, P.E., Silverstein, R.M., Rodin, J.O. (1968). Response of *Ips confusus* to synthetic sex pheromones in nature. *Science* **159**, 1373–1374.

Yearian, W.C., Gouger, R.J. and Wilkinson, R.C. (1972). Effects of the bluestain fungus, *Ceratocystis ips*, on the development of *Ips* bark beetles in pine bolts. *Ann. Entomol. Soc. Am.* **65**, 481–487.