

FOREST-BARK BEETLE ECOSYSTEMS
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FOREST-BARK BEETLE INTERACTIONS: BARK BEETLE POPULATION DYNAMICS

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INTRODUCTION

The intent of this chapter is to organize and interpret the advances in understanding of the population dynamics of the southern pine beetle (SPB), western pine beetle (WPB), and mountain pine beetle (MPB) relative to IPM goals. The specific objectives are to: (1) define the interrelationships between bark beetle population dynamics, host dynamics, and IPM, (2) provide a framework for structuring current knowledge of bark beetle-host systems, (3) identify advancements in understanding of bark beetle population dynamics, and (4) consider the role of the host tree in the population dynamics of these important pest insects.

There have been a number of comprehensive reviews published that deal with various aspects of the population dynamics of the pine bark beetles. These include: SPB (Coulson 1974, 1979, 1980; Coulson et al., 1980a); WPB (Miller and Keen, 1960; Stark and Dahlsten, 1970; Wood and Bedard, 1977;

Wood, 1980a); MPB (Berryman, 1974; Amman, 1978; Cole and Amman, 1980; Stark, 1980; Cole, 1981; Amman and Cole, 1983).

INTERRELATIONSHIPS BETWEEN BARK BEETLE POPULATION DYNAMICS, HOST DYNAMICS, AND IPM

Population dynamics is defined here as the change in distribution and abundance of an organism through space and time. *Stand dynamics* covers change in the density, composition, and age-size structure of trees in forest stands through space and time. These simple definitions are somewhat misleading, as there has been considerable debate and confusion in the ecological and statistical literature regarding precise definitions of the basic parameters of insect and host plant populations. DeMars et al. (1979) provide a review of the concepts applicable to bark beetle-affected forest stands (see Chapter 4 also). Similarly, there are alternative ways of viewing the space and time resolution of bark beetle population systems (Coulson, 1979; Chapter 2).

IPM and its applicability to forests have been defined in several ways (Waters, 1974; Stark, 1977a; Huffaker et al., 1978; Waters and Stark, 1980; Coulson, 1981; Coulson and Stark, 1982). A comprehensive definition contains four key points: (1) the foundation of IPM rests on the principles of ecology and has as its cornerstone the elements of natural control, including the effects of weather, host resistance, and natural enemies on pest populations; (2) the methodology can range from a conscious decision to do nothing to the use of all suitable control tactics, and relies on the establishment of realistic economic thresholds; (3) the functional goal is to obtain optimum benefits with acceptable costs, whether the benefits are measured in terms of timber, water, recreation, and so on; and (4) IPM is a component of, and to be fully integrated into, the total resource management process in both planning and operation (Chapter 2).

In general, a population becomes a pest problem if it is numerous enough to cause significant injury. Forest management objectives and the social and economic values associated with the particular ecosystem being managed will determine the definition of significant injury. Reduced to simplest terms, populations become more numerous by reproduction and immigration and less numerous by mortality and emigration. Therefore, pest population management is directed to holding pest populations at tolerable levels by either lowering reproduction or immigration or increasing mortality or emigration. How these ends are accomplished is discussed in Chapter 6.

Historically, pest management in forests has been synonymous with crisis response, that is, where spatial and temporal coincidence of the pest and host occurred under especially favorable conditions. Most of these attempts failed

or provided only temporary relief. Resource management planning now attempts to avoid (or anticipate) the conditions responsible for pest outbreaks rather than respond to a crisis once it has occurred. Obviously, detailed understanding of both pest and host population dynamics is essential if crises are to be avoided.

FRAMEWORK FOR STRUCTURING KNOWLEDGE ON BARK BEETLE-HOST SYSTEMS

Recent multidisciplinary IPM research and applications programs adopted the use of conceptual and analytical mathematical models as a means of abstracting key features of the population systems for the pine bark beetles (Chapter 1). This approach was particularly beneficial because there was a great deal of existing information on bark beetle populations that had not been systematically organized. Areas of needed new research then were more easily identified. Also, it was anticipated that predictive models of bark beetle population dynamics could be developed that would serve as an integral component of a computer-based decision support system for forest resource management.

The grouping of information about organisms and their interactions in space and time into a series of hierarchical levels is well founded in the basic concepts of ecology (Odum, 1971). In structuring the mathematical models of bark beetle population dynamics, it became evident that they also could be organized into a hierarchy representing different levels of interaction and of complexity (see Figure 2.3). Certain unique information could be derived from each level, and the sum of the information from all levels would serve as the basis for assembling a realistic and reliable set of coupled population dynamics models. Overlap of information between levels can occur and certain types of information can appear in more than one level. However, to facilitate organization of population dynamics information, this hierarchical structure is useful. Following is a brief description of the various levels, and examples of critical information derived from them, relevant to pine bark beetle population dynamics.

The Individual Insect

The first level in the hierarchy consists of the individual insect. For bark beetles, the sequence of life stages involved are parent adult, egg, four larval instars, pupa, callow or teneral adult, and brood adult (Chapter 1).

Most of the research conducted at this level has been carried out under laboratory conditions. These studies have provided basic information on

reproduction (Reid, 1958, 1962b; Amman, 1972a; Ryker and Rudinsky, 1976; Wagner et al., 1981), developmental rates (Reid, 1962a; Gaumer and G. 1967; McCambridge, 1974; Gagne, 1980), fungi-host interactions (Craighead and St. George, 1940; Whitney and Cobb, 1972; Shrimpton, 1978; Raffa and Berryman, 1982), parasitoid-host interactions (Richerson and Borden, 1972; Berisford, 1980; Dahlsten, 1982), and morphology (Cerezke, 1964). Details of individual characteristics are provided in Chapter 1. In general, at the first level, life stage distribution and abundance and related spatial-temporal factors are considered only as factors that modify these processes and characteristics.

Individuals In Infested Trees

The second level in the hierarchy encompasses the successive insect life stages as they occur on or in host trees. This level constitutes what has normally been classified as "natural history." By far, the greatest quantity of information on bark beetles is at this level. Emphasis historically was directed at obtaining information on distribution and abundance of the insects in sample units of host trees, while ignoring precise definition of space and time components. For example, partial life tables based on discrete point estimates have been constructed for WPB (DeMars et al., 1970), SPB (Coulson et al., 1976a), and MPB (Knight, 1959; Cole, 1974; Amman and Cole, 1983). These life tables are based on the assumption that the age distribution of the life stages within the host is stable, which clearly is not the case.

Most field studies of the pine bark beetles have been directed to elucidating population characteristics and events that take place at the second level. Following are several examples of such information: description of specific aspects of the life cycle of the insect (e.g., Miller and Keen, 1960; Amman, 1972; Goldman and Franklin, 1977), identification of parasitoids and predators associated with within-tree populations of *Dendroctonus* spp. (e.g., DeLeon, 1934; Bushing, 1965; Dahlsten, 1970; Berisford et al., 1970; Berisford, 1980), definition of competitive associations (e.g., Cole, 1973, 1975; Coulson et al., 1976a, 1980b), investigation of reproductive strategies (e.g., Reid, 1958; Dudley, 1971; Coulson et al., 1976b), and study of host resistance mechanisms causing mortality (e.g., Reid, 1963; Berryman, 1972; Amman and Cole, 1983).

Attributes of Populations in and Among Infested Trees

The third level in the hierarchy represents essentially the between-tree dynamics of beetle populations, involving dispersal, host selection, concentration, establishment, and emergence and reemergence. At this level, beetle

distribution and abundance in space and time are considered simultaneously for the first time. Population processes at this level have been studied most extensively during the last decade. These studies include the responses of beetles to pheromones (e.g., Pitman and Vité, 1969; Wood, 1972; Borden, 1972; 1982; Coster et al., 1977; Wood, 1982), beetle-fungus-tree interactions (Whitney, 1971; Whitney and Cobb, 1972; Safranyik et al., 1975; Barras and Bridges, 1976; Fares et al., 1980a), and quantitative analysis of within-tree survival rates (e.g. Berryman et al, 1970a,b; Cole et al., 1976; Coulson et al., 1976c; Coulson et al., 1979b; Cole, 1981; Amman and Cole, 1983). However, our knowledge regarding the interrelationships and relative importance of intra- and interspecific competition, natural enemies, symbionts, temperature, moisture, and food quality on within-tree beetle survival still remains incomplete for most beetle-tree associations.

Populations in Infestations and Stands

The fourth level in the hierarchy consists of the expression of the within- and between-tree population processes at the infestation and stand level. This level explicitly includes in-flight mortality as it affects attack rates and patterns (Wood and Bedard, 1977; Gagne, 1980). Again, the space and time components of beetle population processes all operate at this level. For the first time, stand characteristics and dynamics enter the scenario. Site characteristics, such as soil type, can be extremely important. Also, weather conditions and climate patterns (related to geographic location and elevation) further influence the interaction between beetle population dynamics and stand dynamics.

Research at the infestation level is essential in developing fundamental knowledge of the population dynamics of bark beetles and their interactions with host stands. Until recently, a major difficulty in conducting studies at this level was the lack of quantitative estimation procedures with defined accuracy and precision (Pulley et al., 1977b). There are now several different options available (e.g., Carlson and Cole, 1965; Pulley et al. 1976, 1977a, 1979a; Coulson et al., 1979a; Stephen and Taha, 1979a). Because the patterns of infestation growth and development are different for each species of pine bark beetle, generalization from one to another can be misleading.

For pest management, knowledge of beetle population dynamics at the infestation or stand level is critical, since this is the basic operational unit for all prevention and suppression strategies and tactics (Chapter 6).

Populations in Forest Ecosystems

The fifth level in the hierarchy encompasses the expression of the presence of bark beetles in forest ecosystems. Emphasis is directed not to population

numbers *per se*, but rather to their interrelations with and effects on other components of the ecosystems.

Research at this level has been largely theoretical and interpretative. For example, Roe and Amman (1970), Amman (1977), and Peterman (1978) have evaluated the probable ecological role(s) of MPB in lodgepole pine forests. Schowalter et al. (1981a) described the interaction of SPB and fire on forest succession and nutrient cycling in southern forests comprised of shortleaf, loblolly, longleaf, and slash pines. Other studies have dealt with the influence of weather and climate on MPB and SPB distribution and abundance (Amman, 1973; Safranyik, 1978; Gagne et al., 1980). Cole et al. (1976) and Berryman (1976, 1978b, 1982) considered patterns in the epidemiology of MPB. The critical role of WPB, in combination with photochemical oxidants, in effecting changes in succession in mixed conifer forests in southern California has been described by Dahlfen et al. (1980).

It is important to recognize that interpretations at the fifth level involve integration of knowledge from each of the preceding levels. However, experimentation on pine bark beetle populations at the forest ecosystem level is virtually nonexistent, and no IPM strategies have been developed as yet for actual operations.

ADVANCES IN UNDERSTANDING BARK BEETLE POPULATION DYNAMICS

The NSF-EPA funded program on the pine bark beetles and the expanded research and application program of the USDA Forest Service on the southern pine beetle have served as a catalyst in developing new knowledge of the population dynamics of these major forest pests. Knowledge of the population systems of the three *Dendroctonus* species involved differed at the start due to different prior institutional commitments and levels of funding. Much was known of the basic biology and general ecology of each. However, with a common focus on the proposed system for managing them (Chapter 2) renewed efforts were made to fill the voids in key aspects of their population dynamics, and their interactions with the host trees and other components of the pine ecosystems concerned. As previously noted, most of this research was directed at the stand or infestation level, where interactions between the insects and their hosts are most significant from the standpoint of resource management.

Population Sampling

Quantitative sampling methods are essential in the study of insect population dynamics. The reliability of estimates of mortality and survival rates is depen-

dent on the accuracy and precision of estimates of population density at successive intervals. Further insight into the causes of mortality, the interactions among mortality-causing agents or processes, and dispersal characteristics of populations similarly requires valid quantitative estimates of population parameters of interest. Moreover, in studies aimed at the management of pest insects, two further requisites depend on sound quantitative procedures: (1) the development of predictive models of pest occurrence and trends in density, and (2) the development of reliable and practicable methods of population assessment for monitoring. Considerable emphasis has been given in the last decade to this aspect of research on pine bark beetles.

Differences in the biology and behavior of the pine bark beetles require that different sampling designs be used for collecting data on populations. The mountain pine beetle, for example, has just one generation per year; the western and southern pine beetles have two or more generations each year. For the latter two species, the timing of sampling is critical in obtaining discrete population estimates. The distribution of attacks on host trees differs. MPB first infests lower portions of lodgepole and ponderosa pines, then progresses up the tree bole. In contrast, WPB and SPB tend to concentrate on the mid-bole area, with decreasing densities toward the base and live crown. The mountain pine beetle normally completes larval development in the phloem (inner bark), and all stages prior to emergence are easily counted by removing sections of the bark. The other two species occupy the outer bark of their respective host trees in the later larval stages and as pupae, and counting of the insects is more difficult.

A method of sampling and procedures for collecting and processing bark samples for counts of MPB were described by Carlson and Cole (1965); these have been utilized in most of the population studies of this insect. Modifications have been suggested by Shepherd (1965) and Safranyik (1968). Techniques for obtaining quantitative estimates of the WPB were developed by Berryman et al. (1970a), with additional information on the analysis of the data provided by DeMars (1970) and Dudley (1971). A flow chart of the successive samplings needed to quantify the survival of WPB over an entire generation is shown in Figure 3.1. These techniques were subsequently adopted for use in studies of the SPB, with more detailed investigation of the efficiency of various modifications and extensions (Coulson et al., 1975b; Foltz et al., 1976; Stephen and Taha, 1976, 1979a; Pulley et al., 1977b, 1977c, 1979a; Hain et al., 1978; McClelland et al., 1978; Nebeker et al., 1978). Certain of these, for example, the use of host tree geometric models (Foltz et al., 1976) and topological mapping of insect occurrence in infested trees (Pulley et al., 1976) are applicable to bark beetles and their associates in general. The statistical relations of sampling intensity, precision, and informational content are discussed by Pulley et al. (1977a). In a broader context, Coulson et al.

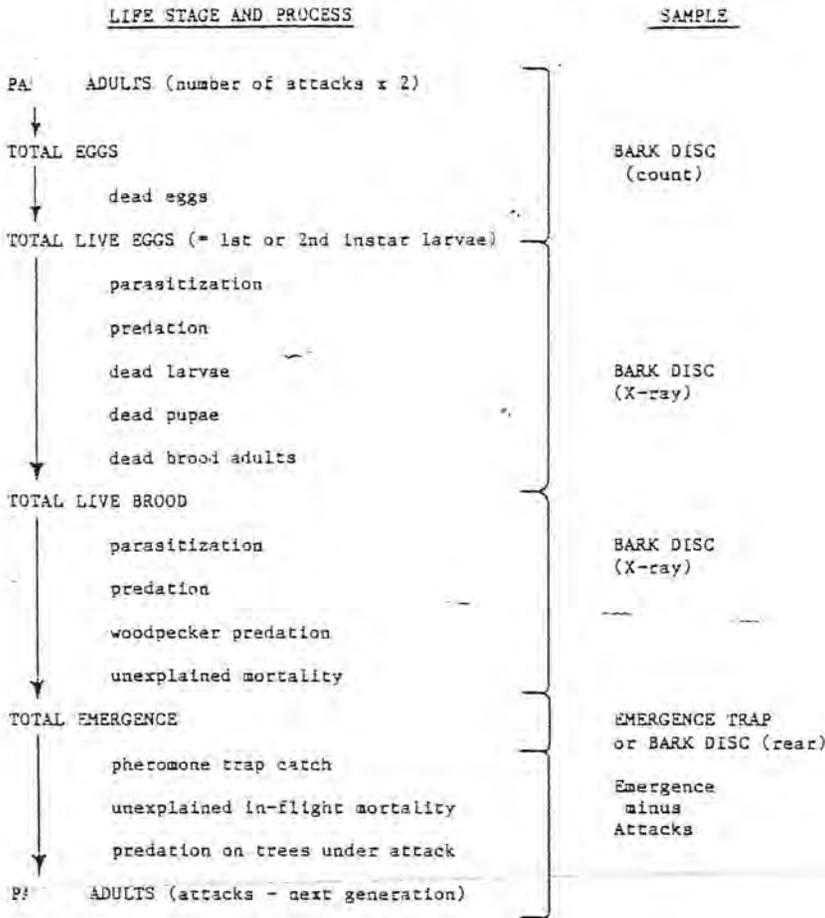


Figure 3.1. Flow chart of successive sample collections for the life stages of the western pine beetle over a single generation.

(1980c) describe a procedure for integrating estimates of SPB densities from attacked trees throughout the course of development of an infestation. This procedure, which is applicable to other bark beetles, provides the basis for quantitative description of the population growth pattern of an infestation (Schowalter et al., 1981b) and coupling this with a stand dynamics or prognosis model (Chapter 4). These sampling methods apply to the third and fourth levels of the hierarchy described above, and thus provide the basis for integrating data from them.

Information on methods of direct sampling of bark beetle populations applicable to monitoring is given in Chapter 7.

Population Modeling

Modeling of the population dynamics of pine bark beetles has been vigorously pursued during the last decade. Knowledge from all levels in the hierarchy is needed for a model to realistically mimic the dynamics of a population system. When one considers all the variables that affect the basic parameters of a bark beetle population, it is not surprising that the modeling approach is extremely useful in organizing and formalizing our knowledge of the system.

Two basic approaches have been taken in modeling bark beetle population dynamics: statistical regression models and biophysical mechanistic models. The *statistical approach* provides one of the best ways of summarizing data collected under changing conditions and subject to random variation. Analysis of data by regression highlights the important variables contributing to system dynamics. However, such a model cannot be applied to conditions other than those in which the original data were collected. The *biophysical approach* requires a search for mechanisms that may account for what is observed. This modeling approach mathematically describes functional relationships and then integrates them into an overall system model. Thus, such a model allows for the prediction of a response outside the range of the original data. Often a combination of the two approaches is used in developing a population model, although most can be classified as either predominantly statistical or biophysical.

In general, the accuracy and precision of predictive population dynamics models have been related to space-time resolution. Best results have been obtained at the infestation or stand level of organization, with a time period ranging from several weeks to several months. Both accuracy and precision diminish as the space and time dimensions are enlarged. This occurs primarily because of uncertainty and imprecision in accounting for changes in weather over long periods of time.

Detailed models of the population dynamics of southern pine beetle (Hines, 1979; Feldman et al., 1980; Hines et al., 1980) and mountain pine beetle (Cole et al., 1976; Crookston et al., 1978) have been constructed. Each of these models is directed to population dynamics in individual infestations and for stands. Essential features of the models of SPB and MPB are outlined below.

Models of SPB Population Dynamics

There are two principal models available that describe the population dynamics of SPB, designated hereafter as the TAMBEETLE model (developed

at Texas A&M University) and the Arkansas model (developed at the University of Arkansas).

The TAMBEETLE model (Feldman et al. 1980, 1981a, 1981b) is a biophysical mechanistic model of the population dynamics of SPB in infestations. The model includes several component submodels that describe individual life stage processes of the beetle. The model also includes consideration of forest stand density and microclimatic conditions. Figure 3.2 illustrates the basic elements and linkages in the model. A user-oriented version has been developed which permits several different options for data input for initialization. Output from the model includes basic information on beetle population numbers, tree mortality, and economic loss (Chapter 4). The model is best suited for predictions over a time span of 1-3 months.

The Arkansas model (Hines, 1979; Hines et al., 1980) is a deterministic simulation model that considers the sequence of beetle life stages as a production process affected by physical and biotic factors in the environment of an infested stand. It includes submodels of the component processes determining beetle productivity and mortality and is formulated as a set of differential equations expressing rates of change in numbers from one stage to the next. The final output is density of emerging adults (Figure 3.3). It can be coupled to stand inventory data to provide predictions of tree losses within a stand on a weekly basis and estimates of the value of cumulative losses incurred (Chapter 4). A user-oriented version of the model has been developed in order to simplify application. As with TAMBEETLE, this model is most reliable for predictions over a 1-3 month time span.

Model of MPB Population Dynamics

The approach taken in simulation modeling for MPB was somewhat different from that employed for SPB. The focal point of the modeling effort was the stand prognosis model for lodgepole pine and associated species developed by Stage (1973) and Wykoff et al. (1982). The population dynamics model of MPB (Crookston et al., 1978) serves as a submodel to the stand prognosis model to provide information on beetle-caused tree mortality in addition to the normal mortality that is calculated by the prognosis model (Chapter 4).

This model (MPBMOD) is a statistical model consisting of two major components: (1) a flight and attack model which includes submodels for emergence, emigration, intertree distribution, flight mortality of the beetles, and effects of aggregation pheromones; and (2) a productivity model which calculates beetle productivity (the ratio of emergence density to attack density) as a function of attack density, tree diameter, total host bark surface area, sex ratio, elevation, and latitude. MPBMOD is an epidemic model with a temporal resolution of approximately 7-12 years, which is the period of duration for most outbreaks of the insect.

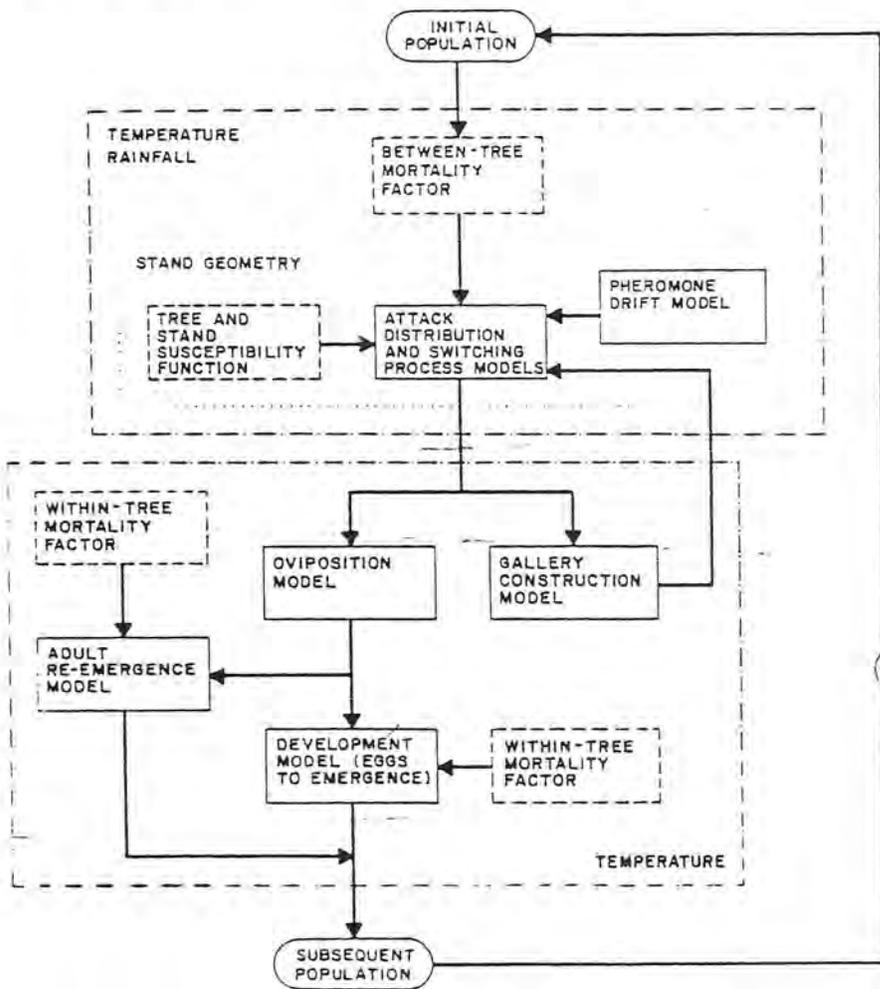


Figure 3.2. Flow diagram of the TAMBEETLE model of SPB population dynamics.

Within-Tree Population Processes

Within-tree populations of SPB, WPB, and MPB have been studied for many years. The goal of modeling populations of bark beetles at this level inspired in-depth investigations of certain basic processes. In particular, developmental rates, reproductive biology, habitat microenvironmental effects, and natural enemy-caused mortality were considered to be of critical importance.

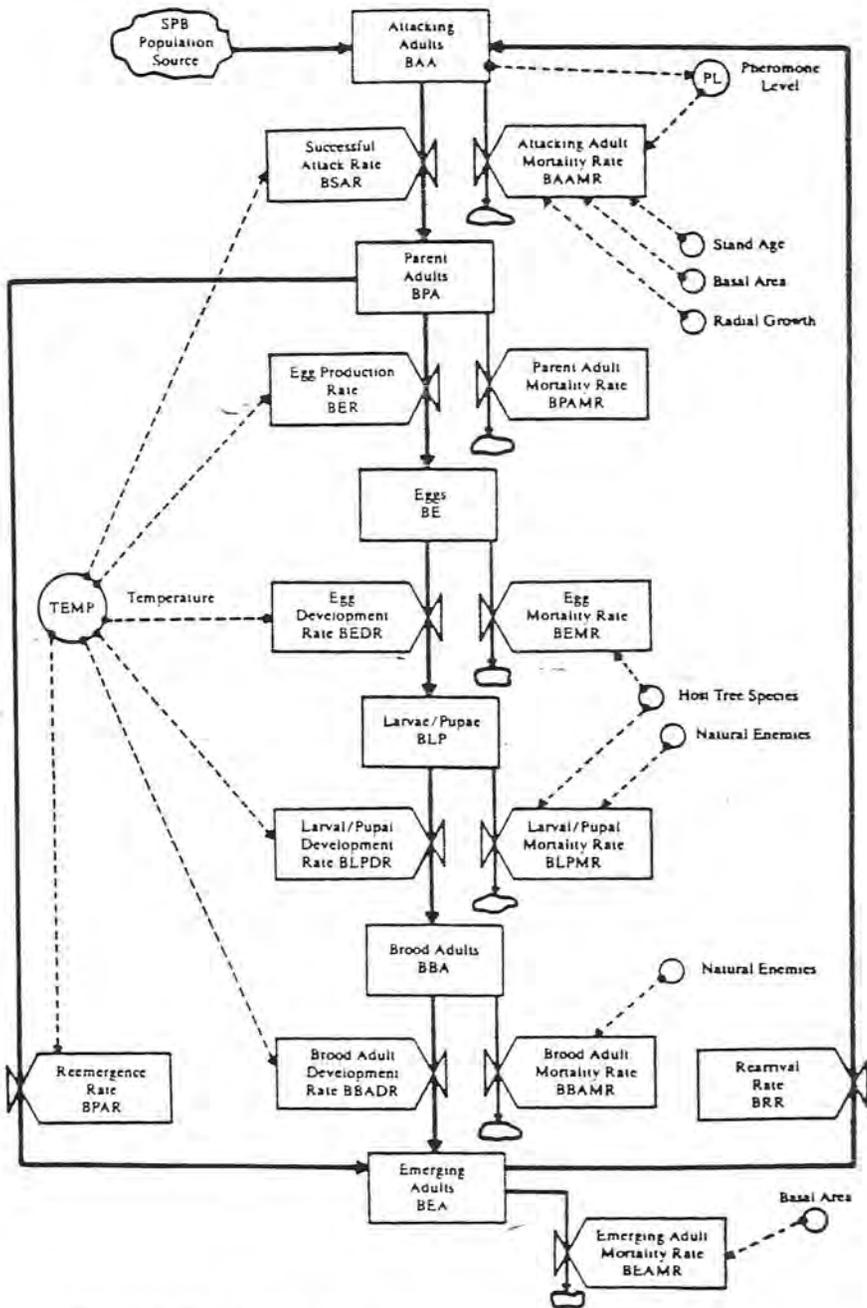


Figure 3.3. Flow diagram of the Arkansas model of the SPB population system.

Information on the developmental rates of SPB and WPB has been difficult to obtain because of problems associated with rearing these beetles consistently under laboratory conditions. In contrast, MPB is reared relatively easily. Detailed understanding of development time is of fundamental importance to modeling population dynamics. Rate functions determine in large part the accuracy of the model. Developmental rates for MPB were determined for both field (Powell, 1967) and laboratory populations (Reid, 1962a; McCambridge, 1974). Wagner et al. (1979) conducted a study of SPB brood development in living trees, and a sophisticated model of poikilotherm development is available for this insect which has a theoretical basis in reaction kinetics (Sharpe and DeMichele, 1977; Gagne, 1980). Predictions of the model realistically portray conditions measured in the field.

Information on reproduction of bark beetles is also of critical importance in modeling their population dynamics. Major advancements in understanding the reproductive biology of the pine bark beetles have been made (Reid, 1962b; Amman, 1972a; Ryker and Rudinsky, 1976; Wagner et al., 1979, 1981). Experimentation indicates that variables such as the density of attacking adults, larval density, season of the year, moisture, temperature, and inner bark thickness all greatly influence reproductive success. Wagner et al. (1980) have developed a model of reproduction for SPB that incorporates many of these variables.

Since bark beetles spend the majority of their lives within the host tree, microenvironment of this medium has a pronounced effect on population growth and survival. Successful attack by pine bark beetles results in death of the host or a portion of it and sets into motion a series of successional changes within the tree. The within-tree habitat is utilized by several hundred different insect and mite species as well as a number of microorganisms. The biota associated with these bark beetles during the within-tree stages have been studied quite thoroughly (Chapter 1). The concept of the dead tree as an ecological unit and the succession of organisms from tree death to nutrient release and recycling has been suggested, but very little work has been done in this area (Graham, 1925; Howden and Vogt, 1951) and the succession of organisms after bark beetle emergence is therefore poorly known.

Once a host tree is successfully colonized, it begins to dry and both the habitat condition and food quality change. Several investigators have documented within-tree habitat changes for the pine bark beetles (e.g., Reid, 1961; Gaumer and Gara, 1967; Powell, 1967; Wagner et al., 1979). The most pronounced and rapid case of habitat change occurs in trees attacked by SPB. This insect can complete development in approximately 35-50 days during favorable weather. Wagner et al. (1979) suggest that the movement of fourth stage larvae to the outer bark is a behavioral response to the worsening conditions of the inner bark. Coulson et al. (1976a, 1980b) state that by moving to

the outer bark, larvae avoid or minimize the results of inner bark foraging by buprestids and cerambycids. Larvae of MPB do not exhibit the same behavior, and therefore sometimes suffer heavy losses from foraging borer larvae (McCambridge et al., 1979). A great deal of the unexplained mortality characteristically observed in bark beetle-infested trees is likely attributable to varying degrees of habitat suitability.

The acquisition of information on the amount and importance of mortality caused by entomophagous insects to pine bark beetles has been slow. Sampling procedures designed for bark beetle populations may not be appropriate for their natural enemies. Either more samples or a larger sample unit area was required to obtain reliable estimates of SPB parasite and predator densities (Stephen and Taha, 1976). Early studies with MPB (Struble, 1942; Schmid, 1970, 1971; Amman, 1972b), WPB (Berryman, 1970; Dahlsten and Bushing, 1970), and SPB (Moore, 1972) provided limited quantitative information on mortality caused by entomophagous species. Linit and Stephen (1983), using exclusion techniques, found that insect parasites and predators may cause at least 25 percent of the total generation mortality of SPB populations within trees. The comprehensive study of natural mortality factors affecting the dynamics of MPB populations in lodgepole pine by Cole (1974, 1975, 1981) has provided a large data base for quantitative analysis of the importance of parasites and predators in regulating the numbers of this insect. Based on the analysis of data for many generations of MPB through several infestation cycles, using a competing risk analysis technique, Amman and Cole (1983) conclude that host-related factors, rather than natural enemies, are most important in regulating beetle densities. The predator *Medetera aldrichii* appeared to have the greatest—though not significant—effect, because it showed a density-dependent response over time and increased effectiveness in larger diameter trees (where beetle production is usually greatest).

Beetle Population Dynamics in Infestations and Stands

The availability of quantitative sampling procedures for within-tree and within-infestation populations and detailed knowledge of the population processes occurring within individual trees have permitted investigation of the space-time dynamics of beetle populations at the infestation or stand level. Successive population estimates of attacks, reemergence, eggs, brood survival, and emergence have provided basic information on the patterns and factors affecting growth and development of populations at the infestation and stand level (DeMars et al., 1970; Cole et al., 1976; Cole and Amman, 1980; Coulson et al., 1980c). The importance of reemergence, which is common for SPB and WPB but not MPB, and reemergence plus emergence (=

allocation, Coulson et al., 1980d) to perpetuation of infestation growth and pattern have been defined (Schowalter et al., 1981b). Furthermore, it has been possible to develop and test various hypotheses on between-tree survival using quantitative estimates of populations of attacking, reemerging, and emerging adults (Coulson et al., 1980d; Pope et al., 1980). Cole et al. (1976) modeled trends in MPB populations in lodgepole pine as a function of changes in host tree size and abundance.

Improved knowledge and explicit models of the spatial and temporal dynamics of pine bark beetle populations in infestations and stands are providing sounder bases for management planning and decision.

Response of Bark Beetles to Behavioral Chemicals

Insect- and host-produced chemical compounds play an important role in bark beetle population dynamics (Chapter 1). For bark beetles to perpetuate themselves, it is necessary that they identify relatively rare susceptible hosts and then aggregate a population of adults large enough to kill the tree or, in the case of MPB, a portion of it. A large number of both insect- and host-produced compounds have been identified and various behavioral roles ascribed to them (Wood and Bedard, 1977; Borden, 1977, 1982; Payne, 1979; Wood, 1982).

Since behavioral chemicals are of great significance in the population dynamics of the pine bark beetles, their functional role(s) must be included in mathematical models (Burnell, 1977). This requirement has necessitated research on the patterns of dispersal of the compounds in forests. Fares et al. (1980c) developed a generic model of pheromone dispersion in forests which takes into consideration the effects of micrometeorological conditions on concentration profiles of the behavioral chemicals beneath the forest canopy. The model was developed from data on SPB and MPB.

Role of the Host Tree in the Population Dynamics of the Pine Bark Beetles

Bark beetle interactions with their host trees take place at levels two through five in the hierarchy presented above. For the purposes of this discussion, emphasis is directed primarily to the third level, that is, in and among infested trees. Interactions at the stand and forest ecosystem levels are considered in detail in Chapter 4.

Host susceptibility to insect colonization and *within-tree habitat suitability* for brood development are critical elements in the population dynamics of pine bark beetles. Both elements are involved inseparably in the interrelation-

ships between beetle population numbers, associated microorganisms, natural enemies, and chemical and physical qualities of the host.

Host Susceptibility/Resistance

Literature on the subject of host susceptibility to the pine bark beetles has been reviewed by Stark (1965), Cobb et al. (1968a, 1982), Berryman (1972), Wood (1972), Safranyik et al. (1975), Amman (1978), Shrimpton (1978), Coulson (1979, 1980), Raffa and Berryman (1982), and Amman and Cole (1983). In the following discussion the terms *host susceptibility* and *host resistance* are used interchangeably.

The colonization process (Rasmussen, 1974; Stephen and Dahlsten, 1976a; Fargo et al., 1978—Chapter 1), when successful, initiates a series of successional events that eventually lead to the death and subsequent degradation of the host. The first step in the sequence involves overcoming tree resistance mechanisms. For *Pinus* spp. the major defense is the resin system. If the colonization phase is successful, the tree, or a portion of it, will die. Without this, the beetle brood will not develop and survive.

Safranyik et al. (1975), Fares et al. (1980a), and Wood (1972) have provided recent insights into the interaction of tree resistance mechanisms, beetle numbers, and fungal inoculum for MPB in lodgepole pine, SPB in loblolly pine, and WPB in ponderosa pine, respectively.

Within-Tree Habitat Suitability

Once tree resistance has been overcome through successful colonization, the suitability of the host tree for brood development becomes important.

Variation in within-tree habitat suitability affects beetle populations in several ways.

1. Phloem thickness or quantity is the most important factor determining MPB brood production in lodgepole pine (Amman, 1972c; Berryman, 1982).
2. The physical characteristics of the host (diameter, outer bark thickness, phloem thickness) affect the rate at which the host (and within-tree habitat) dries (Wagner et al., 1979). Rapid drying of the phloem can result in significant within-tree mortality of small larvae (Cole, 1981; Amman and Cole, 1983), and later stages (Reid, 1961; Fares et al., 1980b; and Gagne, 1980).
3. Physical characteristics of the host influence accessibility by natural enemies. Insect parasites are more numerous in the upper portions of host trees, where the bark beetles are most accessible because of thinner bark (Dahlsten and Stephen, 1974). Woodpeckers, by peeling away much of

the outer bark, may make WPB larvae more accessible to insect parasites, thus greatly increasing parasitism (Otvos, 1965).

4. The chemical qualities of the habitat substrate affect the nutrients available to developing life stages as well as its suitability as a culture medium for microorganisms (Hodges et al, 1968a,b; Hodges and Lorio, 1969; Shrimpton, 1973).

It is important to recognize that host stands (the fourth level of the hierarchy) vary greatly in average tree susceptibility and suitability, and individual stands can change in their average susceptibility and suitability over time. Furthermore, within any stand, the individual trees differ in their susceptibility and habitat suitability at every point in time. At the forest ecosystem level, host susceptibility and suitability are dynamic variables related to the mosaic of conditions existing within the stands that comprise it.

AREAS OF NEEDED RESEARCH

Although a great deal of information about pine bark beetle population dynamics, relative to IPM objectives, has been assembled, there are a number of specific subject areas that are in need of further study. These include (1) primary host selection, (2) bark beetle epidemiology, (3) dynamics of within-tree mortality, (4) within-tree habitat and stand micrometeorology, and (5) biophysical tree models. However, it must be recognized that virtually no single component of the population dynamics of bark beetles is so well understood that further investigation would not be justified.

Primary Host Selection

The process of primary host selection, whereby a small number of adult beetles locate a susceptible host tree and identify it for other beetles, is poorly understood (Chapter 1). Knowledge of the process of primary host selection is of fundamental importance to understanding the process of development of infestations within stands and between stands, and to the development of a rational and reliable predictive model for use in managing these pests.

Bark Beetle Epidemiology

A great deal is known about host, site, and stand variables that contribute to development of outbreaks once beetle populations are established (Chapters 1 and 7). However, basic questions regarding adult beetle longevity outside

the host, dispersal distance, and between-tree (in-flight) mortality have not been adequately answered.

Dynamics of Within-Tree Mortality

The natural enemy and arthropod associates component of the within-tree population systems of the pine bark beetles have not been studied in sufficient detail to adequately determine the functional relationships involved, nor represent them in a predictive population model. Computer simulation experiments that utilize mathematical models of the tree host-insect population system offer an approach to investigating this important aspect of bark beetle population dynamics.

Within-Tree Habitat and Forest Micrometeorology

Micrometeorology of the within-tree and stand habitats has a marked influence on bark beetle population dynamics. Knowledge of micrometeorology beneath the forest canopy is of importance because of the highly developed dependence of bark beetles on perception of behavioral chemicals. Temperature, humidity, and air movement all affect the dispersal of these chemicals. Adult longevity outside the host is determined in large part by temperature (Coulson et al., 1980d; Gagne, 1980).

Some models of the population dynamics of the pine bark beetles are driven by temperature-dependent rate functions (Feldman et al., 1981a); therefore, accurate predictions of meteorological conditions beneath the forest canopy are needed. Generally, weather station information is used as the data source. Correspondence between conditions beneath the forest canopy, within-trees, and weather station data must be defined if model predictions are to be accurate.

Biophysical Tree Models

The several stand growth projection models available for pine species (e.g., Stage, 1973, for lodgepole pine; Daniels and Burkhart, 1975, for loblolly pine) were not developed for the purpose of explaining the complicated interactions of bark beetles and their hosts. There has not been a concerted effort to develop a biophysical model that abstracts basic knowledge of both host plant physiology and subsequent degradation following bark beetle colonization. Fares et al. (1980a,b) have addressed the latter part of the problem, from a theoretical viewpoint, in their "tree drying model."

A more complete biophysical model of insect-host tree interaction would provide a means of investigating a number of basic problems in bark beetle population dynamics, such as (1) hypotheses of primary host selection, (2) the confrontation of bark beetles with primary defense mechanisms of pine species during colonization, (3) processes of fungal inoculation by bark beetles and subsequent death of the host, (4) the large degree of unexplained mortality characteristically observed, and (5) the relationships of within-tree habitat quality and reproduction and developmental rates.

ACKNOWLEDGMENTS

We acknowledge and thank A. M. Bunting for assistance in the preparation of the manuscript for this chapter. Much of the research reviewed in this chapter was conducted through funding provided by NSF project GB 34718, the USFS-SEA Expanded Southern-Pine Beetle Research and Application Program, the USFS Integrated Pest Management Program, the USFS Pacific Southwest Forest & Range Experiment Station and the USFS Intermountain Forest Range & Experiment Station, and the Texas Agricultural Experiment Station (MS 6009).