

MANAGEMENT DECISION-MAKING TOOLS FOR MOUNTAIN PINE BEETLE
(*Dendroctonus ponderosae*) (Coleoptera: Scolytidae) POPULATIONS
IN LODGEPOLE PINE (*Pinus contorta*) STANDS

by

Barbara Joan Bentz

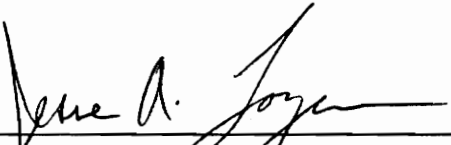
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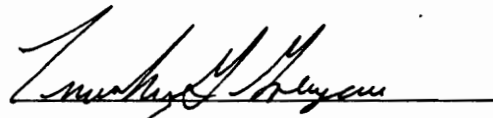
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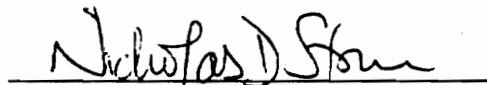
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Committee Chairman: J.A. Logan
Entomology

(ABSTRACT)

To prevent the buildup of epidemic level mountain pine beetle populations, conditions of the stand environment they inhabit must be altered. Silvicultural treatment is the most effective means for doing this. Preventative treatments work best when applied while mountain pine beetle populations are still at the endemic population level. Therefore, information necessary for making decisions concerning mountain pine beetle populations in lodgepole pine stands needs to be included in the initial silvicultural prescription planning process, at a time before beetle populations reach outbreak numbers.

In this dissertation, several quantitative descriptions of the mountain pine beetle/lodgepole pine relationship were investigated. Models were developed to 1) describe the temperature-dependent development of six mountain pine beetle life-stages and 2) describe the amount of loss a stand could sustain if an epidemic level population were to occur in the stand. Concepts of mountain pine beetle risk rating were also discussed. These models and additional information pertaining to the mountain pine beetle/lodgepole pine relationship were incorporated into a knowledge-based system, the MPB Advisory System. This system was designed to help U.S. Forest Service silviculturists include decisions concerning mountain pine beetle populations in the stand management process.

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Table of Contents

Abstract	ii
Acknowledgements	iii
List of Tables	vii
List of Figures	ix
Scope and Objectives	1
Chapter 1. Introduction and Literature Review	
Life History	5
Population Parameters	9
The Host-Lodgepole Pine	11
Mountain Pine Beetle Management in Lodgepole Pine Forests	12
Additional Strategies for Mountain Pine Beetle Management	16
Quantification of the Mountain Pine Beetle in Lodgepole Pine Stands	18
Decision-Making in Forest Pest Management	21
Chapter 2. Temperature-Dependent Development of the Mountain Pine Beetle and Simulation of its Phenology	
Introduction	28
Methods	
Constant Temperature Experiments	30
Phloem Temperature Measurements	31
Developmental Rate vs. Developmental Time	31
Phenology Model Development	33
Results and Discussion	35
Conclusions	38
Chapter 3. An Evaluation of Risk Classification Systems for the Mountain Pine Beetle in Northern Montana and Concepts for Improving Predictions	

Introduction	48
Evaluation of Mountain Pine Beetle Risk Classification Methods	51
Data Description	51
Results	52
Discussion	55
A Logistic Model for Mountain Pine Beetle Risk Classification	57
Methods	57
Results	59
Discussion	60
Conclusions	65
Chapter 4. A Model for Predicting Timber Loss in Lodgepole Stands Due to the Mountain Pine Beetle	
Introduction	80
Methods	
Data Description	83
A Probability Model for Host Tree Infestation	84
Simulating Temporal Tree Infestation	91
Model Validation	92
Results	93
Discussion	93
Chapter 5. An Advisory System for Mountain Pine Beetle Management in Northern Montana	
Introduction	118
Knowledge Acquisition	119
System Development	
Knowledge Representation	122
System Flow	125
Discussion	127
Conclusions	128
Conclusions and Recommendations	142
Literature Cited	148

Appendix I

164

Vita

205

List of Tables

1.1	Knowledge-based system terminology. References used include Coulson et al. 1987, Davis and Olson 1985, Hunt 1986, Plant and Stone 1991, and Random House College Dictionary 1982.....	27
2.1	Functional forms of the developmental rate and distribution models used for describing mountain pine beetle phenology	39
2.2	Estimated parameter values, adjusted r^2 , and sample sizes (N) for developmental rate and distribution models	40
3.1	Descriptive statistics for data used to evaluate the risk classification methods. This data set was also used to estimate parameters for the logistic regression model. The data includes only those stands with a static or declining MPB population trend (see text)	66
3.2	Comparison of observed and predicted results from Amman et al. (1977) system. Low = < 25% mortality, Moderate = 25-50% mortality, and High = > 50% mortality. Mortality is interpreted as the percentage of dead LPP in the stand. Observed and predicted count and share are the frequency and percentage of stands in each category. Proportion successfully predicted is the proportion of stands predicted to be in a certain category which were observed in that category	67
3.3	Comparison of observed and predicted results from Mahoney (1978) system. $PGR \geq 1.0$ indicates mortality $\geq 10\%$, and $PGR < 1.0$ indicates mortality $< 10\%$. Mortality is measured as percent lodgepole pine infested	68
3.4	Habitat type groupings used for determining indicator variables in the regression analysis. Listed for each group are the abbreviations and codes, in parenthesis, for each habitat type in that group. Groupings are based on Vegetation Management Guidelines in the Forest Management Plan, Flathead National Forest	69
3.5	Parameter estimates and goodness of fit statistics for logistic regression model. Data used to estimate parameters is described in Table 3.1. CCF = crown competition factor, LPQMD = lodgepole pine quadratic mean diameter, HAB1 and HAB2 = habitat indicator variables, %BALP = percent of the basal area in lodgepole pine, ID1 and ID2 = stand indicator variables	70
3.6	Stand and site variables identified to be associated with mountain pine beetle caused lodgepole pine mortality. Variables are categorized by the systems in which each is used	71
4.1	Initial stand characteristics (year 1 of the study) based on 10 year permanent plot data from northern Montana. Plots which were harvested during the study are not included. TPA = trees per acre, BA = stand basal area (sq.ft./acre),	

	LPTPA = lodgepole pine trees per acre, LPBA = lodgepole pine basal area, and QMD = quadratic mean diameter (inches)	96
4.2	Descriptive statistics for data used to estimate logistic model parameters. This data is a subset of the data described in Table 1 and is denoted by (E). Values are based on plot-level densities. N is the total number of observations in the data set, which may include up to 10 years for any given tree. See Table 1 for stand location and habitat type. TPA = trees per acre, LPTPA = lodgepole trees per acre, BA = stand basal area (sq.ft./acre), LPBA = lodgepole pine basal area, DBH = diameter at breast height (inches)	97
4.3	Descriptive statistics for validation data. This data is a subset of the data described in Table 1 and is denoted by (V). Values are based on plot-level densities. N is the total number of observation in the data set, which may include up to 10 years for any given tree. See Table 1 for stand location and habitat type. TPA = trees per acre, LPTPA = lodgepole trees per acre, BA = stand basal area (sq.ft./acre), LPBA = lodgepole basal area, DBH = diameter at breast height (inches)	98
4.4	Parameter estimates and goodness of fit statistics for logistic regression model. Parameters were estimated for pooled data and for data ranked by 2 inch (") diameter class. LPTPA = lodgepole pine trees per acre, LAG1 = number of infested trees the previous year, INDIVBA = individual basal area (sq.ft./acre), Year = year of infestation, ID1, ID2, ID3 = stand indicator variables	99
5.1	United States Forest Service personnel interviewed during the knowledge acquisition process	131
5.2	Silvicultural treatment options identified in the knowledge acquisition process to be useful for reducing losses caused by the mountain pine beetle	132

List of Figures

- 2.1 Residual values (observed days minus predicted days) using model TM2 (see Table 2.1) with observed time data, developmental rate data, and the least squares estimate weighted with $1/\text{rate}^2$ 41
- 2.2 Developmental time functions for eggs, larval instars, and pupae fit to median times at constant temperatures. Equations and estimated parameters for developmental functions are in Tables 2.1 and 2.2. Curves represent the time (in days) to complete the life-stage at each constant temperature42
- 2.3 Predicted cumulative probability of emergence for eggs, larval instars and pupae compared to observed normalized values. Equations, estimated parameters, and sample sizes for distribution functions are in Tables 2.1 and 2.243
- 2.4 Average phloem temperatures measured on the north side of a 25.1 cm dbh lodgepole pine in the Sawtooth National Recreation Area, ID infested with mountain pine beetles44
- 2.5 Density in each life-stage predicted by the phenology model using phloem temperatures from an infested lodgepole pine in the Sawtooth National Recreation Area, ID. The model was initiated with 100 eggs on day 22245
- 2.6 Density of larvae in Instar I, Instar II, and Instar III showing the temporal synchrony predicted by the simulation model. The phenology model was initiated on day 222 with 3 recruitment levels of egg cohorts: 1 cohort (100 eggs laid on a single day), 10 cohorts (100 eggs laid over 10 days), and 20 cohorts (100 eggs laid over 20 days). Note the difference in time scale between instars47
- 3.1 Crown competition factor as a function of percent trees per acre lodgepole pine (%LPTPA) infested on the Flathead National Forest. Values are an indication of the MPB population trend at the time of the initial survey (1984)72
- 3.2 Trees per acre lodgepole pine (TPA) infested by the mountain pine beetle in 3 forests in northern Montana. Current trees per acre infested the year of the survey (1984), the previous year (1983), and 3 years prior (Older) are combined to provide a 5 year cumulative total (Total)73
- 3.3 Observed percent basal area lodgepole pine killed as a function of crown competition factor (CCF) (Schenk et al.1980)74
- 3.4 Observed percent basal area lodgepole pine killed as a function of Stand Hazard Rating (SHR) (Schenk et al. 1980)75
- 3.5 Observed percent lodgepole pine basal area killed as a function of stand resistance as defined by Berryman (1978)76

3.6	Comparison of observed and predicted results from a logistic regression model using density values calculated at the plot level. Values are observed and predicted proportion trees per acre lodgepole pine infested	77
3.7	Standardized residuals of observed and predicted proportion trees per acre infested in each stand of the Lolo, Kootenai, and Flathead National Forests. Predicted results are from the logistic regression model described in the text...	78
3.8	Components of the dynamic relationship between MPB populations and LPP stands. Two separate phases are important: 1) the transition from the endemic to epidemic population level, and 2) the growth of an outbreak population resulting in tree loss. The two phases are dependent, in part, on different stand characteristics. A circle represents the transition probability	79
4.1	Observed trees per acre (TPA) infested in permanent plots in Stand 1 (Kootenai National Forest). See Table 4.1 for stand description	101
4.2	Observed trees per acre (TPA) infested in permanent plots in Stand 2 (Lolo National Forest). See Table 4.1 for stand description	102
4.3	Observed trees per acre (TPA) infested in permanent plots in Stand 3 (Flathead National Forest). See Table 4.1 for stand description	103
4.4	Observed trees per acre (TPA) infested in permanent plots in Stand 4 (Flathead National Forest). See Table 4.1 for stand description	104
4.5	Predicted number of trees infested from the simulation model, averaged over the number of runs of the model. Based on this graph, 50 runs of the model was determined to be an acceptable number for predictive purposes. Average trees infested changed less than 1/4 of a tree after that number	105
4.6	Observed and predicted trees per acre (TPA) infested by year for Stand 1. Predicted results are from Logistic and Cole models using data described in Table 4.3	106
4.7	Observed and predicted trees per acre (TPA) infested by year for Stand 2. Predicted results are from Logistic and Cole models using data described in Table 4.3	107
4.8	Observed and predicted trees per acre (TPA) infested by year for Stand 3. Predicted results are from Logistic and Cole models using data described in Table 4.3	108
4.9	Observed and predicted trees per acre (TPA) infested by year for Stand 4. Predicted results are from Logistic and Cole models using data described in Table 4.3	109
4.10	Observed and predicted trees per acre (TPA) infested by dbh class for Stand 1, all years combined. Predicted results are from Logistic and Cole models using data described in Table 4.3	110

4.11	Observed and predicted trees per acre (TPA) infested by dbh class for Stand 2, all years combined. Predicted results are from Logistic and Cole models using data described in Table 4.3	111
4.12	Observed and predicted trees per acre (TPA) infested by dbh class for Stand 3, all years combined. Predicted results are from Logistic and Cole models using data described in Table 4.3	112
4.13	Observed and predicted trees per acre (TPA) infested by dbh class for Stand 4, all years combined. Predicted results are from Logistic and Cole models using data described in Table 4.3	113
4.14	Percent difference, (observed - predicted)/observed, trees per acre infested by Stand and diameter class. Class 1 = 5.0-7.0", class 2 = 7.1-9.0", class 3 = 9.1-11.0", class 4 = 11.1-13.0", class 5 = > 13.0". Predicted results are from the Logistic model	114
4.15	Percent difference, (observed - predicted)/observed, trees per acre infested by Stand and diameter class. Class 1 = 5.0-7.0", class 2 = 7.1-9.0", class 3 = 9.1-11.0", class 4 = 11.1-13.0", class 5 = > 13.0". Predicted results are from the Cole model	115
4.16	Total observed and predicted trees per acre (TPA) infested (by Stand) for 10 years. Model predictions are from the Logistic and Cole models	116
4.17	Percent difference, (observed - predicted)/observed, in residual basal area in each Stand after a 10 year MPB outbreak. Predicted results are from the Logistic and Cole models	117
5.1	One section of the knowledge network graph representing the declarative knowledge of silviculturists on the Flathead National Forest. Each node is a concept or proposition describing some part of the stand prescription process. Nodes are linked by relations. LPP = lodgepole pine, QMD = quadratic mean diameter	133
5.2	Function model of the decision process used in determining silviculture treatments for lodgepole pine stands when the mountain pine beetle is an influencing factor. Each box describes a separate decision which must be made before determining the overall goal, the optimal silvicultural treatment option. Rounded boxes represent decisions which are solved using quantitative models, and square boxes have rule-bases associated with them. Information flow required for each decision is represented by arrows	135
5.3	An example of the frame-based knowledge structure used in the MPB Advisory System. A frame is used to describe a general class of objects, such as Stand_Information. Flathead_01234 is a specific instance of Stand_Information with slot values which store specific data pertaining to the stand	136

5.4 Hierarchical frame structure for the MPB Advisory System. Each box represents a frame and the associated instances with that frame. Top Frame is a Goldworks system structure inherent in all applications developed with this software. ?'name' symbolizes a variable137

5.5 Knowledge structure of the rule-base. Stand and MPB population information, and treatment option are used to estimate the quality of the residual stand and economic concerns. The optimal treatment provides the best (Good) of both constraints 138

5.6 Example of the reasoning structure for the Regeneration Harvest treatment option. Rules shown are for 'good' residual stand and 'good' economic concerns only. When the attempt is queried, the backward-chaining goal-rule searches for a pattern to match each part of the rule consequent. The enabling pattern in the Rule-Sets match these patterns, and rules within the sets are then fired. If these rules are satisfied, control is sent back to the goal-rule and the AND-THEN part of this rule is fired, resulting in the answer being placed in slots of the final-report instance140

5.7 Example summary output file from the MPB Advisory System. Output is for hypothetical stand '1234' on the Flathead National Forest141

C.1 Proposed additions to the MPB Advisory System. Additional components which would increase the efficiency and predictive capabilities of the decisions currently made by the system are shaded grey. Circles represent external models accessed by the system. Refer to Figure 5.2 for a detailed description of the existing function model147

Scope and Objectives

The mountain pine beetle (*Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae)) is a native component of the lodgepole pine (*Pinus contorta* Douglas) ecosystem and plays an important role in determining the succession of the surrounding forest. Due to the eruptive nature of mountain pine beetle populations however, endemic populations can rapidly increase to the epidemic population phase. Outbreak populations often cause extensive damage, both economic and aesthetic. Many resources in a forest may be influenced including timber, water, wildlife, and recreation. To effectively manage lodgepole pine stands, managers must consider the influence of mountain pine beetle populations on stand resources before the population reaches the outbreak phase. Once this phase is reached, control over wide areas is not feasible.

Preventative management for the mountain pine beetle does not entail direct management of the beetle population. To adequately arrest the growth of an outbreak beetle population, one must alter the environment of the beetle, i.e. the stand structure. The most effective means for doing this is to use silvicultural treatments. Several silvicultural strategies (partial cutting, etc.) have been found to be successful in preventing the development of outbreak mountain pine beetle populations in lodgepole pine stands. By using strategies like partial cutting, managers can alter the stand structure while mountain pine beetle populations are still in the endemic phase. In most cases this makes the stand environment less favorable for further population growth to the epidemic level. For many reasons, however, not every stand can be treated in this manner. To prioritize stands for silvicultural treatment, the manager

needs to be able to identify those stands with conditions most favorable to mountain pine beetle populations, and that have the greatest likelihood of becoming heavily infested. To do this requires methods which can associate beetle-caused mortality with particular stand and site characteristics.

The goal of this research was to incorporate strategies for mountain pine beetle management into the current decision process used by Forest Service resource managers. The use of silvicultural treatments as a preventative measure is currently limited to only a few managers who have the knowledge necessary for making the required decisions. Several models have been developed that assess the expected mortality in a stand due to the mountain pine beetle, thereby enabling the manager to target those stands for treatment. However, improvements to these models as well as further quantitative descriptions of the mountain pine beetle/lodgepole pine relationship were needed. Several objectives were pertinent to fulfilling this research goal:

1. Describe and model the temperature-dependent mountain pine beetle phenology. Knowledge of this relationship will aid in understanding trends in climate-related population growth and development.
2. Evaluate and enhance existing models for determining the susceptibility of a lodgepole pine stand to a mountain pine beetle infestation.
3. Evaluate and enhance existing models used by silviculturists to determine the expected amount of timber to be lost over time due to the mountain pine beetle.
4. Define the current decision process for stand management used by silviculturists on a National Forest in northern Montana which takes

into account strategies for reducing timber losses due to mountain pine beetle populations.

5. Develop a computerized framework which links the quantitative and qualitative information necessary for managing lodgepole pine stands for mountain pine beetle populations. The developed system can then be used as an aid for determining the most appropriate silvicultural treatment to alleviate mountain pine beetle population growth and utilize currently infested timber.

Chapter 1. Introduction and Literature Review

The mountain pine beetle, *Dendroctonus ponderosae*, was described by Hopkins in 1909, as was the black hills beetle, *D. monticolae*, in 1902. These two species were later combined (Wood 1963) to form one species, retaining the scientific name *D. ponderosae* and common name mountain pine beetle (MPB). The MPB has a wide geographic distribution, occurring from British Columbia (56° latitude) to northwestern Mexico, and from the Pacific Ocean east to the Black Hills of South Dakota (Safranyik et al. 1974). MPB populations may be found from sea level in British Columbia to 11,000 ft. in Colorado. Unmanaged stands¹ of mature and overmature lodgepole pine, ponderosae pine, western white pine, sugar pine, whitebark pine and limber pine are the most susceptible to attack by the MPB (Amman and Cole, W.E. 1983). The most frequently infested host is lodgepole pine (*Pinus contorta* Douglas), comprising 95% of all trees killed by the MPB in the Western United States (McGregor 1985a). MPB populations infest extensive areas of lodgepole pine and most likely have always been a component of the lodgepole pine ecosystem (Peterman 1978). Because MPB behavior often varies with the host tree species in which brood develop, the focus of this study was restricted to the response of MPB and only one host, lodgepole pine.

¹ A stand is a homogeneous aggregation of trees with uniform composition, age, and spatial arrangement. A group of stands comprise a management unit.

Life History

The MPB interacts with its host at 3 levels of complexity: the individual tree, and the distribution of these trees throughout the stand and forest. The individual tree is the basic population unit, and to date, much research has been directed at MPB biology in lodgepole pine trees (see Cole, W.E. and Amman 1980, Amman and Cole, W.E. 1983, Raffa 1988, and Reid 1960 for reviews). The MPB is a univoltine species which attacks living pines, and unlike most phytophagous insects, successful reproduction is usually contingent upon host mortality (Wood 1973). Strip attacks however, whereby only one side of the tree is attacked, may also produce successful brood. The ability of MPB to colonize live hosts is in part facilitated by their mutualistic relationship with microbial phytopathogens (Craighead 1928). MPB may require 2 years to complete a generation at high elevations or northern latitudes, although a 1 year life-cycle is the norm (Amman 1973). The MPB life-cycle can be divided into three phases: dispersal, colonization, and development. Except for a short, but critical, flight period during dispersal and colonization, MPB complete their entire life-cycle in the phloem of the host tree.

Dispersal of insects is often viewed as an adaptive trait enabling survival in uncertain and heterogeneous environments (Wellington 1980). For the MPB, dispersal is one of the least understood yet most important aspects of its population ecology (Safranyik et al. 1989). The MPB dispersal phase begins with emergence from the brood tree, and is influenced by weather conditions, especially temperature, and possibly chemical attractants (Gara and Vite 1962, Rasmussen 1980, Safranyik and Jahren 1970). Emergence requires several days of relatively warm temperature, and maximum flight activity occurs between 11:00 am and 5:00 pm. Depending on

elevation and latitude, the flight period usually begins in late July and continues into August, with the greatest concentration occurring during a 3 week period (Reid 1962).

Colonization includes selection of a susceptible host (Raffa and Berryman 1980) and aggregation of individuals on the new host. This process is mediated by a complex pheromone system which involves numerous semiochemicals, some of which seem to send the same message (Borden and Lindgren 1988, Borden et al. 1990). Females, the homogametic sex (Stock and Amman 1980), are usually responsible for locating the new host and seem better able to withstand the environmental stress associated with being the pioneer gender (Amman and Pace 1976). During the early stages of flight, suitable hosts are often located using a combination of random landings guided by visual cues, and followed by chemical and tactile cues once on the host tree (Hynum and Berryman 1980). This hypothesis is supported by experiments in which large, dark objects were more attractive to MPB than small, dark objects (Schonherr 1976, Shepherd 1966). Rasmussen (1972) found that beetles preferred large diameter trees over small diameter trees baited with the attractant semiochemicals *trans*-verbenol and alpha-pinene. Additionally, Bennett and Borden (1971) found that an obligatory flight prior to an olfactory response to host stimuli is common in some bark beetle species. Gara et al. (1984), however, observed that flying MPB were attracted to host volatile materials in the early dispersal phase, counteracting the theory of random landings. Observations by Roe and Amman (1970) also suggest that beetles may use chemical cues to select a host. Among trees of similar diameter, beetles chose the thicker phloem trees which also contain greater quantities of terpenes. Due to the volatile nature of monoterpenes, this may be the olfactory stimulus drawing beetles to larger diameter, thick phloem trees (Cole, W.E. et al. 1981).

According to the Hynum and Berryman (1980) theory, after arrestment on a tree, beetles may initiate feeding and either be repelled by non-host terpenes, or accept the feeding stimulus as host material. If the beetle is repelled, flight continues until a suitable host is found. Upon selection of a suitable host, the female bores a hole into the bark, and through a chemically mediated synergistic reaction with host chemical compounds, she releases *trans*-verbenol, an aggregation pheromone which primarily attracts males (Pitman 1971, Pitman et al. 1968). Males produce *exo*-brevicomine which at low concentrations primarily attracts females (Conn et al. 1983, Borden et al. 1987). This system of chemical communication enables a massive aggregation of individuals on a single tree which, for MPB populations, is selectively advantageous in overcoming host defensive mechanisms.

Only after the dispersing female has located a suitable host will she feed and thus accumulate a store of nutrients necessary for egg production. In this manner, nutrients stored during the larval period can be used for dispersal, which helps to maintain adaptive variation in the species. The initial feeding by adult beetles elicits a defensive response by the host tree in an attempt to resist colonization by the MPB. This induced resistance is a combination of static and dynamic defensive processes that attempt to isolate the attacking beetle and its symbiotic blue-stain fungi (Shrimpton 1978, Miller and Berryman 1986). Attacking beetles may become mired in the resin exudation from resin ducts severed during feeding, a phenomena called pitching out. The more resistant, vigorous trees respond by forming greater quantities of resin than successfully attacked trees (Raffa and Berryman 1982), thereby pitching out a greater proportion of the attacking population. Almost all trees will respond to an invasion, but only those with a rapid and sustained reaction are most likely to survive. Because *trans*-verbenol is an oxidized product of host defensive compounds, beetles

will be attracted as long as the tree is capable of secreting resin. If many beetles attack the same tree over a short period of time, they may exhaust the tree's defensive mechanisms. The resin flow will be depleted sooner than in a lightly attacked tree, thus ensuring a successful colonization by the beetle population, no matter what the resistance capability of the tree. The final outcome of a colonization attempt therefore, is dependent upon a series of competing physiological rate reactions which regulate both beetle arrival and host responses (Raffa and Berryman 1980).

Because establishment of the next generation only occurs when the defenses of the new host are sufficiently overcome, it is advantageous for many beetles to attack the same tree. As with most herbivores however, there is an optimal density range of individuals on an exhaustible food resource. If densities are too high, mortality can result from within-tree competition (Cole, W.E. 1981). The term epideitic describes specific sorts of animal behavior which are used principally for population density regulation (Prokopy 1980). Verbenone, an epideitic pheromone, is released by attacking males to inhibit the landing of additional beetles at that site on the host tree when densities become too great (Borden et al. 1987). Flying beetles in the area will switch to adjacent host trees producing the characteristic spot infestations (Geiszler et al. 1980).

Mating occurs under the bark, and eggs are laid in a long vertical gallery in the phloem. Depending on the temperature, eggs will hatch in approximately ten days (Logan and Amman 1986). Larvae then mine outward at right angles to the axis of the egg gallery, girdling the host tree as they mine.

Development in all life-stages is highly dependent on temperature (Safranyik, 1978, Wygant 1942, Amman and Cole, W.E. 1983). Because the eggs, smaller instars, and pupae are highly susceptible to extreme cold temperatures, larger instars (III and IV) are the optimum life stage for entering winter, the dormant period. Winter

temperatures are thought to be the greatest mortality factor to developing MPB populations (Cole, W.E. 1981). Once temperatures become warmer in the spring, larvae continue developing, pupate, and emerge the following summer as mated or unmated adults to repeat the cycle. Life-history strategies for avoiding excessive winter mortality and increasing survival during other times of the year are discussed in Chapter 2.

Population Patterns

Many factors influence MPB population dynamics, the most important being: tree age and vigor, tree diameter, phloem thickness, habitat, and climate (as described by elevation and latitude) (Amman et al. 1977, Cole, D.M. 1985, Cole, W.E. and Amman 1969, Cole, W.E. and Amman 1980, Shrimpton 1978). Most research in these areas has been directed at epidemic population levels. MPB populations may persist in an endemic state for many years in small pockets, but because minimal tree mortality occurs, these low level populations have not been the focus of extended research. Although the factors responsible for the rapid buildup of population numbers to outbreak proportions are not clear, once an epidemic is initiated, it is generally accepted that populations are food-limited (Amman 1984).

One of the major differences between the endemic and epidemic phases is the physiological state of the host trees which beetles attack. Endemic MPB populations are often concentrated in smaller-diameter, suppressed and diseased trees which are often also infested with associated bark beetles (Schmitz 1988, Tkacz and Schmitz 1986, Kulhavy et al. 1984). Such trees may have previously been weakened by environmental stress factors such as fire, lightning, or drought (Beal 1934, Berryman 1976, Gara et al. 1985), and are usually less vigorous and unable to resist attack by the low numbers of beetle present. Less vigorous trees typically have thinner phloem

(Cabrera 1978), which will also influence the number, size, and sex of the beetles produced (Amman and Pace 1976). Thicker phloem trees are typically larger in diameter and provide more high quality food for the developing brood, and tend to produce larger and more beetles (Amman 1972). Although the thick phloem trees are usually more resistant to low level beetle attacks, if they experience a decline in vigor caused by environmental stresses, the concomitant reduction in resin production would allow successful colonization by a relatively small number of beetles (Berryman 1976). Additionally, the thicker phloem would provide optimal conditions for brood development, resulting in an increase in the number of beetles produced. The hypothesis that stress is a major factor in the transition from endemic to epidemic populations is supported by this line of reasoning.

During the epidemic phase, high densities of MPB are capable of overcoming the defenses of normally resistant trees by rapid and highly concentrated attacks (Safranyik et al. 1975). In this manner they are functionally able to expand their own food supply. In other words, their ability to colonize trees is a function of the number of beetles in the area. The functional expansion of their food supply has been described as an essential feature of the switch between endemic and epidemic population levels (Raffa and Berryman 1980). As the local density of flying beetles increases, a small infestation may expand to the epidemic phase in a healthy, vigorous stand. MPB show a strong preference for lodgepole pine trees with a diameter greater than 20 cm diameter at breast height (dbh) (Cole, W.E. and Amman 1969). Once started, outbreaks in even-aged stands will usually kill almost all host trees greater than 20 cm dbh, beginning with the larger diameter trees. An epidemic usually lasts about 6 years, depending on weather, site and stand conditions. Once the larger diameter trees in a stand have been killed, smaller trees with thinner phloem are

attacked. Thin phloem in combination with excessive drying under the bark results in higher brood mortality and a collapse of the outbreak (Cole, W.E. et al. 1976).

Essentially, mountain pine beetle outbreaks are limited to those stands with an adequate food supply (large trees with thick phloem) and climatic conditions suitable for reproduction.

The Host - Lodgepole Pine

Lodgepole pine forests, which often form monospecific stands, dominate much of the montane environment from Colorado to Northern Alberta. Lodgepole is a serotinous species which usually depends on recurring disturbances such as fire to regenerate. Ecologically, lodgepole is typically described as a seral species with low shade tolerance, although it can assume several different successional roles in a forest, including climax. Successional trends are frequently interrupted by fire whereby original stands are replaced with essentially pure lodgepole pine stands (Pfister and Daubenmire 1975). In fact, most lodgepole pine forests in the Rocky Mountains were established as a result of fire (Lotan et al. 1985). Due to environmental gradients and varied successional stages of the landscape, however, lodgepole pine forests often display considerable structural variability (Fahey and Knight 1986), consequently great ranges exist in stand density and volume in these stands. Stand spacing may range from open to dense depending on the disturbances which occurred prior to regeneration, and the origination of the seed source. Dense stands which are susceptible to growth stagnation result from rapid juvenile growth and a large seed production (Alexander 1986). All lodgepole pine stands, except those at high elevations, may eventually become susceptible to MPB attack. This hypothesis is based on the long history of co-evolution between lodgepole pine and the MPB (Sturgeon and Mitton 1982). As a stand matures, resistance to the beetle decreases, increasing the

probability of widespread beetle infestations. Beetle damage creates fuel (dead trees) which leads to fire, which in turn leads to lodgepole pine reproduction. In this manner, the MPB uses lodgepole pine for its own reproduction, while at the same time propagating the reproduction of its host (Peterman 1978).

Shifting of resources among community components is proposed to be important for the persistence and stability of a forest ecosystem (Coulson and Stark 1982). Results from a study by Romme et al. (1986) suggest that MPB outbreaks enhance the complexity and diversity of a lodgepole pine community by re-allocating the resources among the structural components of the ecosystem. Before an outbreak, biomass and productivity are concentrated in the dominant canopy. Afterwards, resources are distributed more evenly among the three forest strata: canopy, understory and ground layer. These data also support the supposition that ecological changes due to MPB populations are beneficial to the long-term nature of lodgepole pine stands. Additionally, endemic MPB populations may act as a natural thinning agent in lodgepole pine stands (Graham 1963).

Mountain Pine Beetle Population Management in Lodgepole Pine Forests

U.S. Forest Service silviculturists have traditionally been responsible for managing the forest to obtain sustained high yields of forest crops (Stoddard 1968). In response to legislative and public mandates however, substantial changes have occurred in forest management and planning processes during the past few decades. Many interacting and often conflicting concerns must now be included in the decision-making process. As a result of the National Forest Management Act of 1976, the Forest Service is required to implement a systematic planning process, which includes a silvicultural treatment prescription for every stand. Management objectives (e.g.

timber, recreation, wildlife), silvical characteristics of the tree species, site conditions and economics all influence the choice of a silvicultural prescription. Once a treatment based on timber has been prescribed, a second diagnosis is performed by an interdisciplinary team which includes specialists from many areas such as wildlife, recreation, and hydrology. All team members must agree on the treatment for each stand and National Environmental Policy Act requirements must be met. The final prescription for the stand includes justification stating how the silvicultural treatment chosen will meet the management goals for the stand, taking into account the available resources.

Strategies for prevention of MPB population outbreaks were typically not included in the silvicultural process until the early 1980's. Although forest pest management using silvicultural means had been advocated for many years (see Allen 1988), forest managers initially tried to eradicate MPB populations in lodgepole pine stands (Klein 1978). Direct control methods such as felling and burning, spraying individual trees with a variety of chemicals, and blasting proved to be expensive in time, effort, and resources, and often only provided a short-term solution to the problem (Safranyik 1982, Amman and Baker 1972). It is now known that in most cases, direct control of an MPB outbreak is impractical after an outbreak has started. Moreover, susceptibility of the stand remains the same after chemical control efforts because stand characteristics remain essentially the same. By the early 1970's, it was realized that to successfully cope with the beetle on a long term basis, it would be necessary to change the condition of susceptible stands, and not simply reduce existing beetle population densities. Preventative strategies to keep MPB population levels low were needed.

Clearcutting became the silvicultural treatment of choice (Roe and Amman 1970). Because of the short-lived nature of lodgepole pine and the relatively high expense of harvesting small diameter logs, clearcutting is often the best alternative economically (Alexander 1986). Additionally, breaking up continuous lodgepole pine stands into smaller patches that vary in age and size decreases the potential for extensive, widespread damage due to the MPB (Roe and Amman 1970). However, concern for other forest resources (i.e. riparian areas, wildlife, watershed protection and aesthetics) has limited the amount of clearcutting allowable (The National Environmental Protection Act of 1969). In environmentally sensitive areas where resource objectives other than timber production are important, a reduced level of clearcuts will be the only way land managers can maintain other resource objectives at a desirable level. Toward this goal, researchers have identified silvicultural strategies useful in managing stands to prevent MPB population buildup, and to utilize dead or infested trees. These include: 1) clearcutting in patches to create age, size and species mosaics, 2) salvage cuts to mitigate losses in stands currently being attacked, and 3) sanitation thinning or partial cuts to improve the health of a stand. In some situations, the appropriate option may be simply to defer any kind of treatment in the stand until the next planning phase.

Thinnings may provide economic benefit by removing valuable green timber, yet also increase the productivity and economic value of the residual trees. Additionally, thinnings increase forest diversity, enhance water quality, and modify hiding, and thermal and forage covers important to wildlife (Cole, D.M. 1989). Furthermore, it has become apparent that thinnings may also decrease the susceptibility of a stand to MPB damage by altering stand characteristics which are advantageous to the beetle. Several reasons for this have been proposed. Bartos and Amman (1989) suggest that

alterations in stand microclimate such as increases in temperature, sunlight penetration, and wind speed reduce habitat favorability for MPB. In general, open stands are less susceptible to MPB infestations (Amman et al. 1988b). Others contend that the most important factor in stand susceptibility is a reduction of tree vigor and associated resistance to MPB attacks (Berryman 1982, Shrimpton 1978, Waring and Pitman 1980). From this viewpoint, thinnings provide individual trees with more growing space which increases tree vigor and thereby increases the resistance of the stand to MPB population outbreaks (Keen 1958, Mitchell et al. 1983).

Partial cutting (Alexander 1986), was first tested in 1972 as a means to reduce losses to MPB populations (Cahill 1978). Treatments in that study reduced losses by removing all the large diameter trees, which provide the most food for MPB populations. This type of approach is generally not satisfactory because only poor quality trees are left, and the future value of the stand is reduced. Subsequent efforts have attempted to achieve a desired remaining basal area in a stand by making different levels of diameter limit cuts and thinnings (Hamel 1978, Bollenbacher and Gibson 1986, Amman et al. 1988a, Amman et al 1988b, McGregor et al. 1987). These studies demonstrated that partial cutting successfully reduces beetle-caused mortality and also provides for a desirable residual stand. Mortality due to the MPB is significantly reduced for at least 5 to 10 years following cutting (McGregor 1985b). These treatments work best in areas where beetle levels are low or moderate. Salvage cutting is used in stands undergoing a beetle epidemic. Clearcutting small areas in a patchwork pattern, where applicable, reduces losses by decreasing stand homogeneity and creating a diversity of tree age, size and species throughout the forest (Roe and Amman 1970).

The success that has been realized in using silvicultural measures for preventative MPB management demonstrates that this type of approach may be a

viable option that will meet the demands of forest managers (Cole, D.M. 1989, Gibson 1989). Additionally, for the most part, silvicultural treatments do not increase the susceptibility of the stand to other pests and pathogens (Raffa 1988). In general these strategies aid in producing a diverse forest mosaic which is considered necessary for avoiding widespread outbreaks. To be advantageous in the long-term however, these treatment strategies must be compatible with overall forest management objectives and emphasize biologically sound sustained yield silviculture (Cole, D.M. 1989, Safranyik 1982). For example, lodgepole pine in the Rocky Mountains is considered susceptible to windthrow after partial cutting (Alexander 1986). Therefore, particular landscape characteristics which are indicative of a high risk to blowdown need to be included in the decision process for selecting a treatment. Constraints on harvesting schedules such as market values for timber, allowable cut for a particular forest, and road access must be contended with as well. Not all potential timber losses to the MPB may be harvested due to environmental or economic constraints. Appropriate tools to prioritize stands for treatment, based on risk to an MPB outbreak are therefore important components of the forest management process.

Additional Strategies for Mountain Pine Beetle Management

Semiochemicals have also become a valid option for protecting stands from extensive losses to the MPB. Semiochemicals are naturally occurring compounds produced by individuals of a species that elicit a behavioral response in other individuals of the same or different species. Kairomones are a type of semiochemical which benefit the receiver (Hagen et al. 1984). In the case of the MPB, kairomones released by a host tree are a selective advantage to the beetle. For the MPB, semiochemicals are usually effective only in slowing down an epidemic rather than

preventing one. However, this holding-action allows managers to delay harvesting until constraints (e.g. market values, allowable cut, road systems) are mitigated. Three semiochemicals are responsible for MPB aggregation (Borden and Lindgren 1988): the female-produced *trans*-verbenol, male-produced *exo*-brevicommin, and myrcene, a host-tree kairomone which acts as a synergist for the beetle-produced compounds. Verbenone is an anti-aggregative pheromone which is produced to prevent excessive population density on a single tree. Verbenone is derived from any of three sources: female beetles, autoxidation of α -pinene, and microorganisms (Borden et al. 1987). Traps baited with semiochemicals may be used to determine the presence or absence of MPB populations and the beginning and duration of their emergence period. The greatest use of semiochemicals to date has been to concentrate and contain infestations in a stand which is scheduled for silvicultural treatment (Borden and Lacey 1985, Gray and Borden 1989, Borden et al. 1983, Schmid et al. 1989). Aggregation pheromone baits are placed throughout a stand, enticing MPB to attack trees within the boundaries of the stand. Before the next flight season, trees which have been attacked and infested are harvested and removed.

Anti-aggregative pheromones have also been tested as a management strategy. Initial experiments were conducted to assess whether verbenone could prevent concentration of MPB populations in blocks where trees had also been baited with MPB attractants (Amman et al. 1989, Lindgren et al. 1988, Schmitz and McGregor 1990). In these studies, verbenone-treated plots had significantly fewer infested trees than plots with only MPB baits. Subsequent efforts have attempted to ascertain the optimal application rate of the synthetic verbenone and to elucidate possible variation in MPB response due to varying stand and MPB population densities (Amman et al. 1991). Results suggest that verbenone has the potential to prevent MPB infestations from

reaching unacceptable levels in high-value lodgepole pine stands as long as the population pressure is not too great. Additionally, in Montana MPB population levels did not increase in areas adjacent to treated plots, suggesting that the verbenone effect extends further than the stand being treated (Gibson et al. 1991). In ponderosa pine (*P. ponderosae* Lawson) however, verbenone capsules have not been effective in repelling MPB at any dosage level (Bentz et al. 1989, Lister et al. 1990).

Early studies by Reid (1963) and Cole, W.E. (1981) suggested that parasites and predators were not very effective regulating factors of MPB populations at high densities. However, experiments by Miller et al. (1987) demonstrated that extraregional and exotic predatory insects possess the necessary ecological and behavioral characteristics to be considered as potential biological control agents for the MPB. Pooled data from their cross-attraction studies suggested that *Enoclerus lecontei*, a MPB predator, was attracted to the MPB aggregating pheromone. Chatelain and Schenk (1984) were able to increase the number of clerid predators, *Thanasimus undatulus*, on host trees by baiting them with frontalinal. Additional work in areas of prey-pheromone and predator-kairomone specificity may reveal that biological control could be a viable option for integrated MPB management.

Quantification of the Mountain Pine Beetle in Lodgepole Pine Stands

To use preventive silvicultural measures, silviculturists must consider the available options while stands are still young and include them in long-term planning strategies. Making these decisions requires the silviculturists to integrate quantitative and qualitative information. To prioritize stands for treatment, managers must have the ability to recognize particular stand characteristics which are preferred by MPB populations (Graham 1959) and have an understanding of the effect of the MPB on

these stand attributes. Clearly, all the anticipated losses due to the MPB cannot be prevented.

The majority of attempts to describe MPB/lodgepole pine interactions quantitatively have been theoretically based and fitted to empirical data. Burnell (1977) developed a dispersal-aggregation model based on several theoretical assumptions and then fit the model to field data sets. Berryman (1976) developed a model describing MPB production based on an analyses of basic biological processes in the MPB/lodgepole pine system. Berryman has also used theoretical models to investigate the effect of MPB populations on forest ecosystems (Berryman et al. 1984). Raffa and Berryman (1986) developed a simulation model to examine the interactions between host and beetle populations. Model simulations suggested that factors regulating host vigor are important for maintaining beetle populations below outbreak thresholds. Geizler et al. (1980) developed a model which simulates the daily number of MPB attacks on a focus tree. This model is based on the emission rate of *trans*-verbenol in a stand, beetle density, and measures of tree repellence and resistance. Results from their model demonstrated that population density is important in determining beetle attack behavior. Using life-table data, Cole, W.E. et al. (1976) developed a model which characterized the relationship between host tree diameter and beetle production. These models have been valuable for evaluating the theoretical dynamics of the MPB in lodgepole pine stands and have provided insight applicable to management endeavors. Additional studies on MPB population dynamics include a phenology model describing temperature-dependent development of MPB eggs (Logan and Amman 1986) and a model describing the development of MPB eggs, larvae, and pupae (Chapter 2). MPB contagion has also been modeled using several different approaches (Polymenopoulos and Long 1990, Hamilton et al. 1985, Safranyik et al.

1989). Because the basic nature of MPB dispersal remains unclear, more work needs to be done to advance our understanding of the basic processes governing dispersal and more clearly elucidate the theories these models are based on.

Further endeavors included the development of models that could be used by forest managers to predict MPB behavior in a particular stand. Several hazard and risk rating methods based on indices of vigor, tree size, tree age, and climate have been developed to help land managers determine which stands are most likely to be infested by an MPB population (see Mahoney 1978, Amman and Anhold 1989 and Shore et al. 1989 for reviews). Although McGregor et al. (1981) noted good success with a system developed by Amman et al. (1977), the majority of the developed systems have shown sporadic predictive capabilities. Cole, W.E. and McGregor (1983) developed a model which attempts to quantify the amount of loss a stand will sustain once beetles are present in the stand. This model proved inadequate for predicting losses on three forests in Montana (Gibson personal communication), although in Idaho it predicted volume lost more accurately than two other damage models (Cameron et al. 1990). In a validation test in Oregon, the model underestimated survival in the largest diameter classes and overestimated survival in the smallest (Gillespie et al. 1990). These two validations were based on one year of stand and beetle data which were backdated using the Stand Prognosis Model (Wykoff 1985), rather than actual infestation counts over many years. Modeling efforts for predicting susceptibility and loss expected will be discussed in more detail in Chapters 3 and 4.

Forest managers often use growth and yield models designed to simulate the growth of a stand of trees for a particular species. The Insect and Disease Damage Survey (INDIDS) is a computer program developed to compile stand information and calculate measures of volume, growth, and loss due to MPB (Bousfield et al. 1985).

Mathematical models accessed in this program include the rate-of-loss model developed by Cole, W.E. and McGregor (1983). Although this model was shown to be inadequate on some forests, output from the INDIDS program is currently used by forest managers on several National Forests in Montana. Due to the complex nature of the MPB/lodgepole pine relationship, adequate predictions are not always possible, and managers feel the results from these models are better than no guidelines at all. Attempts to alleviate problems associated with this model will be discussed in Chapter 4. INFORMS, a Forest Pest Management Technology Development Project, is currently being developed to integrate pest management considerations into project-level planning (McNamara and Davis 1990). This system encompasses a wide range of management resource conditions for many pests. The Prognosis growth model (Wykoff 1985) and several of the same insect models included in INDIDS are used in INFORMS.

Decision Making in Forest Pest Management

The United States Forest Service manages and protects several million acres of land for multiple uses. Managed resources include timber, recreation, fish and wildlife, minerals, water, wilderness, and range. Although a single forest ecosystem is not uniformly managed for each of these resources, forest planning is a difficult process. The multiple resources available in a forest and varied public interests must be balanced over a long time-span. The information that forest managers must comprehend spans several disciplines, making it difficult for any one manager to master all the areas. In particular, many forest managers have little knowledge of or experience with forest pests such as the MPB. These managers must depend on forest pest specialists to provide them with strategies for incorporation into their already complex decision processes. In addition, the effectiveness of management is a function

of how well the manager makes use of available knowledge (Rykiel et al. 1984). Efficient transfer of knowledge from research to management in a timely, usable fashion is critical, therefore, to proper forest management. Computers have emerged as useful aids in this process. Advances in computer technology in the past few decades have made it possible to store, retrieve, and manipulate quantitative information and to apply models for solving complex problems in pest management (Coulson et al. 1987). More recently, computer techniques have been developed to solve complex problems using artificial intelligence reasoning methods which are not limited to problems which are numerically tractable, but take into account qualitative information as well. Knowledge-based systems are an example of these new technologies (Table 1.1).

A knowledge-based system is a collection of facts and rules that symbolically represent the knowledge specific to a particular task (Davis 1986). These systems are different from conventional databases in that they deal with knowledge about a defined problem domain rather than just data. A knowledge-based system not only stores data, but interprets and relates it to other information in the system to provide advice on a particular problem (Latin et al. 1987). Expert systems, the most common type of knowledge-based system, contain a knowledge-base which describes the thought processes a human expert uses to solve a problem (Plant and Stone 1991). This knowledge implies an understanding which has been gained from years of experience. Expert systems usually contain specific knowledge pertinent to solving only a particular problem, rather than a lot of general information (Mills 1987).

Expert systems contain two main components: the knowledge-base and the inference engine (Davis 1986). There is a clear separation between these two components. The knowledge-base contains all the domain-specific information which may be represented in a variety of ways including rules, frames, cases, scripts,

semantic nets, and procedures (Plant and Stone 1991). The inference engine is the part of the system containing elementary problem-solving logic which operates by searching through the knowledge base and applying rules, for example, to the current data, thereby accumulating new information. In rule-based systems, the most common type of expert system, the inference engine uses the rules to reason either forward from observations to conclusions, or backwards from a goal hypothesis to the data that might refute the hypothesis (Davis 1986). Human experts do not merely follow a set of rules, however, but are able to choose an appropriate solution by perceiving meaningful relationships which are not necessarily logically related (Hart 1986). In rule-based systems therefore, rules may be regarded as a manifestation rather than a representation of the expert's knowledge (Efstathiou et al. 1986). Rule-based systems work best in decision processes where calculations and comparisons are required, rather than domains where experts must exhibit holistic understanding (Pfeiffer 1989). Integrating pest decisions into components of the forest management process fit many of these guidelines.

The advantages of knowledge-based systems in forest pest management over conventional computer programs are numerous. Knowledge-based systems may incorporate external routines or daemons, often quantitative algorithms, which are not a direct part of the reasoning process but provide needed information (Plant and Stone 1991). In this manner, integrated knowledge-based systems act as a framework to bring together the different and often uncertain components needed for making complex forest pest management decisions. Because they solve problems by chaining logical rules together, these systems have the capability to explain the chain of reasoning used to solve a problem. Explanations are usually determined by tracing the rules that fire during the course of a problem solving session (Brachman et al. 1983).

This mechanism provides the capability for an expert system to be used as a tutorial. This capability is especially important for forest pest management in the United States Forest Service where managers are often transferred into regions where pests they are unfamiliar with must be considered in the management process. Expert systems often are most useful for taking over the more routine aspects of a managers job (Stock 1987). For silviculturists this includes writing prescriptions for stands with very common attributes. A tool designed to recommend silvicultural prescriptions, such as an expert system, would free up the managers time to deal with stands in areas that have special problems. Additionally, expert systems help to preserve and organize scarce knowledge for use by others. For example, silviculturists could benefit by gaining access to knowledge gained by others concerning the proper management of lodgepole pine stands in a particular region. From a research viewpoint, knowledge-based systems provide a framework to help organize and synthesize information of different types pertinent to making a decision (Plant and Stone 1991). In this aspect expert systems also provide insight into determining areas which need additional research.

Any management tool or computer system not designed with the user in mind may very well never be used. Anticipated users of the developed system need to be included in the initial project design to help identify the scope and purposes of the system (Gordon et al. 1987). Also, a system which requires information that a manager does not already have access to will not be as readily accepted, if ever. Users want information that is consistent with their perception of the problem, and they want it in an accurate, user-friendly atmosphere. Systems designed to produce a series of recommendations with associated information from which the manager can make the final judgement have been more successfully accepted than programs which attempt to

replace the user (Stock 1988). Expert systems are best used as a tool to support decisions, not take responsibility for them (Hart 1986).

Research in expert systems for forest pest management has a short history. Only a few systems have been developed (or are currently being developed) for use in forest insect management. The Integrated Southern Pine Beetle Expert System (ISPBEX) was designed to help Forest Service personnel make better decisions when managing forests for the southern pine beetle (*Dendroctonus frontalis* Zimm.) (Flamm et al. 1991). PREDICT is an expert system for diagnosing pest damage of red pine stands in Wisconsin (Schmoldt and Martin 1989). INFORMS, Integrated Forest Resource Management System, is being developed for use in the forest planning process (McNamara and Davis 1990). The goal of the last system is to provide Forest Service managers with an integrated user interface for tools such as GIS, databases, expert systems and simulation models. The intended scope of INFORMS is very general and broad, including aspects of many forest pests. GYPSES, Gypsy Moth Expert System, is currently being developed to aid resource managers in making decisions concerning gypsy moth control tactics in the Northeast (Ravlin et al. 1990).

MPB is an inherent component of the lodgepole pine ecosystem, and cannot be controlled by any single method over extensive areas of land. Timber management in the past century has interfered with the natural cycle and co-evolved relationship between lodgepole pine and MPB populations and will continue to do so in the years to come. Where the management objective is to optimize timber production, man and the beetle are in direct competition. It is now realized that the only practical option for reducing widespread tree losses to the MPB in lodgepole pine forests is to establish a unified management program which incorporates the probability of MPB populations reaching epidemic levels into the long-range forest planning process. The

consequences of not implementing the available options at an early stage are widespread losses of economic and aesthetic benefits. Knowledge-based expert systems are a viable option for integrating the complex information necessary in this process. Downing and Bartos (1991) have developed an expert system for describing endemic MPB population behavior. A knowledge-based system developed to include strategies for MPB management in the timber management process of lodgepole pine stands in Northern Montana is discussed in Chapter 5. The system described in chapter 5 synthesizes specific models and information described in the previous chapters. Chapter 2 discusses a phenology model for temperature dependent MPB development. Chapter 3 is an evaluation of previously developed hazard/risk rating models using data from 3 forests in Northern Montana. A model which estimates the amount of timber a stand will lose due to MPB populations is described in chapter 4.

Table 1.1 Knowledge-based system terminology. References used include Coulson et al. 1987, Davis and Olson 1985, Hunt 1986, Plant and Stone 1991, and Random House College Dictionary 1982.

Fact: Something known to exist or have happened.

Data: A collection of facts made up of either numeric (quantitative) or alphabetical (qualitative) characters.

Information: Interpreted or processed data.

Knowledge: Interpretable or interpreted information in context, i.e. information which has been processed. Declarative knowledge refers to objects and events, and procedural knowledge is information about courses of action.

Domain: A topical area or region of knowledge.

Knowledge-based system: A computer program that applies specialized knowledge to the solution of problems within a specified domain.

Expert system: A knowledge-based system that is designed to emulate the reasoning process of human experts in a particular domain.

Integrated knowledge-based system: A computer system that integrates techniques used in systems analysis and simulation modeling with principles of knowledge-based systems.

Chapter 2.

Temperature-Dependent Development of the Mountain Pine Beetle and Simulation of its Phenology

Introduction

The mountain pine beetle (*Dendroctonus ponderosae* Hopkins), a univoltine species that infests living pines, is a common insect pest in stands of lodgepole pine (*Pinus contorta* Douglas). Adults generally attack susceptible hosts in late July, bore through the bark into the phloem tissue, and construct vertical egg galleries. Larvae emerge and feed upon the phloem tissue, usually killing the host tree. Beetles typically overwinter as third- or fourth-instar larvae which resume development in the spring. Pupation occurs in early summer followed by a teneral adult stage shortly before adult emergence in late July or early August. Due to climatic effects, more than one year may be required for a generation at high altitudes or extreme northern latitudes (Amman 1973).

All life-stages of the mountain pine beetle are exposed to a changing habitat due to alterations in the chemical and physical composition of the host tree (Berryman 1972; Langor 1989) and the surrounding microclimate (Bartos and Amman 1989). Moisture, food availability, resin pressure, predator/parasite complexes, and temperature are factors that influence mountain pine beetle phenology. Of these, the effect of temperature has been studied most extensively. Temperature affects the physiological events that regulate cold-hardiness and largely determines the rate of development for each individual. Early studies (Beal 1934; Bedard 1940; Yuill 1941; Wygant 1942) revealed seasonal and regional differences in cold-hardiness among

mountain pine beetle life-stages, as well as considerable variation among individual mountain pine beetle larvae in their resistance to cold temperatures.

Studies by Amman and Cole (1983) suggest that each larval instar has a unique developmental threshold. Although extreme winter temperatures are thought to be the most important mortality factor of mountain pine beetle populations (Cole, W.E. 1981), the indirect effects of stand microclimate may also strongly influence the timing of critical life-history events and probably play an important role in determining survival of the population. To understand more fully how microclimate affects mountain pine beetle populations, it is necessary to investigate each life-stage separately. Due to the cryptic habitat of bark beetles, however, measuring development in response to temperature is difficult. Consequently, typical approaches in bark beetle studies have not considered variation among the larval instars. Other than the model of mountain pine beetle egg development by Logan and Amman (1986), descriptions of the influence of temperature on the mountain pine beetle have been restricted to general observations and degree-day models for egg hatch (Reid and Gates 1970), general larval development (Amman and Cole 1983; McCambridge 1974; Safranyik and Whitney 1985), and adult emergence (Powell 1967; Reid 1963). This approach, in which all larval instars are combined, is adequate in habitats where effects on the development of each life-stage is constant or the development of each life-stage is consistent throughout the life cycle. Neither of these situations is necessarily true for the mountain pine beetle.

Because the relative temporal distributions of insect life-stages often play a vital role in the survival of a population, understanding the phenology of insect development is central to the study of population dynamics, as well as to pest management concepts. The objectives of this study were to: (1) describe the temperature-dependent

phenology of the eggs, larval instars, and pupae of the mountain pine beetle, and the inherent developmental variation due to microclimate; (2) use these data to develop a simulation model of mountain pine beetle phenology; and (3) test hypotheses concerning mountain pine beetle life-history strategies using the developed simulation model.

Methods

Constant Temperature Experiments

Green lodgepole pine in the Wasatch National Forest, UT, were cut into billets and brought to the laboratory at Ogden, UT. Circular pieces of bark, 20 mm diameter, were cut from each billet. Seven to 10 small holes, simulating egg niches, were cut into the phloem tissue of each bark circle. Newly-emerged females from billets cut in the same stand were allowed to oviposit in green logs. The bark containing the egg gallery was then removed and eggs were extracted using a sterilized teasing needle. One mountain pine beetle egg was placed into each artificial niche, and the bark disk then was placed phloem side down into a Petri dish. To keep the bark disk flat and tightly compressed against the bottom of the Petri dish, a circular piece of plywood and the dish lid were placed on top and secured with several strong rubber bands. Bark disks were placed in humidifiers over a saturated solution of potassium sulfate that maintained relative humidity near 100% and prevented drying of the phloem. Five to six eggs oviposited during the previous 24 h were placed in each bark disk. The disks were then placed in incubating chambers, six at each of 11 different temperatures (5, 8, 10, 12.5, 15, 17.5, 20, 22.5, 25, 27.5, and 30°C).

After egg hatch, individual larval development was checked twice daily. Larval moults were determined by the head capsule color and size (Reid 1962; Amman and

Cole 1983). Occasionally, some larvae submerged into the phloem tissue and observations were not made until they resurfaced. Additionally, not all individuals survived at all temperatures. Therefore a complete developmental history was not available for each individual at each temperature. Because only a few individuals survived to the fourth larval instar, the experiment was repeated. In the second experiment, the disks were placed at room temperature until individuals moulted to the third-instar. After that time the disks were placed in incubating chambers at the 11 temperatures noted above and individuals were observed and development recorded until pupation to the teneral adult occurred.

Phloem Temperature Measurements

Phloem temperatures were recorded (21X Micrologger, Campbell Scientific) in a 25.1 cm dbh (diameter at breast height) beetle-infested lodgepole pine in the Sawtooth National Recreation Area (SNRA), ID (43°53'N latitude, 114°50'W longitude, 2260 meters). Temperatures were recorded hourly, 1.37 meters from the base of the tree on the north and south sides of the bole, from day 221, 1989 to day 219, 1990.

Developmental Rate vs. Developmental Time

Developmental rate is defined as the inverse of the time required to complete an instar or life-stage. Traditionally, for both conceptual and computational convenience, insect phenology models have used a physiologic time-scale based on rate, as opposed to the originally measured developmental time. However, there are several problems associated with using the inverse of time (rate), rather than time itself when estimating model parameters (Kramer et al. 1991). One problem is in the least-squares estimation technique, where the error between observed and predicted values is minimized.

Because of the nonlinearity of the rate transformation ($1/\text{time}$), minimizing the error between observed and predicted developmental times is not the same as minimizing the error between the associated developmental rates. When rate data are used, a disproportionate amount of weight is given to values at temperatures where faster developmental rates occur. For example, the difference between two slow rates (0.01 and 0.02) is 0.01. The difference in time associated with these rates is 50 days. At higher temperatures where faster rates occur (e.g., 0.28 and 0.29), the rate difference is the same (0.01), but the associated error in time (0.123 days) is quite different. Therefore an error in developmental time does not coincide with the same error in its inverse, developmental rate, at all temperatures.

To overcome this problem, a weighted least squares estimation procedure, using $1/\text{rate}$ or $1/\text{rate}^2$ as the weight on the squared residuals, can be used (Wagner et al. 1984). An alternate solution is to estimate parameters using the inverse of the chosen developmental function fitted to the original developmental time data. An example using the Logan TM2 developmental rate model (described in Table 2.1) and developmental data from MPB larval-instar I is shown in Figure 2.1. This figure illustrates the residuals from model parameters estimated from both developmental rate and developmental time data, compared with the residuals from a least-squares estimation weighted with $1/\text{rate}^2$. At low temperatures, residuals from parameters estimated from developmental time data were smaller than those from either the model estimated using rate data or the $1/\text{rate}^2$ weighted least-squares estimation. At higher temperatures, results from the three methods were similar. These observations suggest that when development at low temperatures is important or when development occurs over a long time span, fitting developmental functions to time data should produce a

more accurate representation of phenology. I therefore estimated parameters for the developmental models described in the next section using time data.

Phenology Model Development

The response of insect development to constant temperatures has been studied extensively. Several functional forms representing the shape of the developmental rate curve have been well documented and generally accepted enough to be considered canonical forms (Logan 1988). Many are phenomenological functions, whereby the parameters have descriptive interpretation such as a high temperature development threshold. Therefore, in developing the MPB phenology model my objective was not to statistically determine the shape of a function fitted to data, but to estimate the parameters of specified, well known functions that best describe particular data sets.

Median developmental times for mountain pine beetle eggs, larval instars and pupae were fitted to one of eight previously derived developmental models included in the Population Model Design System (PMDS) (Logan 1988). As described above, the inverse of the developmental function was fitted to the developmental time for each life-stage. Parameters were estimated by least squares. Knowledge of MPB life-stage behavior, such as previously reported low temperature thresholds, and a comparison of the adjusted coefficient of determination (r^2) (Kvalseth 1985) were both used to decide on the best developmental model for each life-stage.

Individual variation among mountain pine beetles was incorporated using a distribution model based on the "same-shape" approach of Sharpe et al. (1977) (further described in Wagner et al. [1984]). The basic assumptions for this method are that the variances of normalized developmental times for each individual are equal across all the temperatures, and the normalized development times have the same distribution at

each temperature. Therefore, when normalized, the curves for each temperature assume the same shape and one cumulative probability distribution can be used. The distributions of developmental times at each temperature were normalized by dividing each observation by the median developmental time at that temperature, producing one curve representative of all temperatures. These data were then fitted to one of three distribution models (Table 2.1). Parameter estimation for both developmental and distribution models was accomplished using the PMDS (Logan 1988).

A cohort is defined as the individuals in a particular life-stage that are approximately the same chronological age, or, in the model, the individuals that enter a particular life-stage during the same simulation time step (Logan et al. 1979). Transfer of individuals from one life-stage to the next is based on advancement of physiological age, which is defined as the cumulative physiological time since the cohort was initiated. Physiological age at time t , which is a combination of calendar time and temperature, is defined as:

$$P(t_1) = \int_{t_0}^{t_1} R[T(\tau)] d\tau$$

where $P(t_1)$ is the physiological time at calendar time t_1 , and R is the development rate, which is a function of temperature (T), which in turn is a function of τ , the variable of integration. The PMDS (Logan 1988), which uses an algorithm based on this cohort concept, was used to develop a simulation model describing the temperature-dependent development of 6 MPB life-stages. See Logan 1988 for a more detailed description of PMDS.

Results and Discussion

Temperature thresholds and developmental time for the egg, larval, and pupal life-stages were derived from the controlled constant-temperature rearing experiments. Using this information, a temperature-dependent phenology model was developed using the PMDS (Logan 1988) that simulates mountain pine beetle development. The selected developmental and distribution models and estimated parameter values for each life-stage are listed in Tables 2.1 and 2.2. The associated fits of the functional forms to observed data are in Figures 2.2 and 2.3.

Optimum temperatures for development in the egg, and larval instars I, II, and III were between 23 and 27°C (Fig. 2.2). In the constant temperature experiments, excessive mortality in the latter life-stages (instar IV and pupae) resulted in a lack of data, and optimum temperatures were not revealed for these two life-stages. However, the optimum temperatures in the earlier life-stages agree with findings by Reid and Gates (1970) and Safranyik and Whitney (1985). In laboratory experiments, Safranyik and Whitney (1985) observed that 30.2 days were required for the mean development from egg to adult at a constant 24°C; Whitney and Spanier (1982) reported 28.29 days. Initiating the phenology model with 100 eggs and simulating development at a constant 24°C produced similar results, although slightly faster development occurred. Fifty percent of the individuals reached the teneral adult stage after 26 days.

Phloem temperature measurements in an infested lodgepole pine provided information about the environmental conditions experienced by developing mountain pine beetles (Fig. 2.4). Results from model simulation using these hourly phloem temperatures are depicted in Figure 2.5. The model was initiated with 100 eggs on day 222, which was during the time when beetles were dispersing to new hosts in the stand. The duration in each life-stage is governed by the phloem temperatures

occurring during that time period. The occurrences and peaks of the life-stages depicted in Figure 2.5 seem reasonable, and similar situations have been observed in field situations (G.D. Amman, personal communication).

Results from the constant temperature experiment revealed that the advanced life-stages (larval instars III, IV, and pupae) required higher temperatures for development than did eggs, instar I, or instar II (Fig. 2.2). Additionally, eggs, and larval instars I and II were able to develop over a much wider temperature range. These results and previous observations (Amman and Cole 1983) indicate that temperature-dependent development is different for each of the mountain pine beetle life-stages examined. I hypothesize that this interaction between temperature and development synchronizes larval instar moults and adult emergence. The evolution of this life-history strategy may serve to maximize mountain pine beetle fitness in a constantly changing environment. Two particular advantages may result from this interaction.

First, higher temperature thresholds of development in larval instars III and IV can prevent progression to advanced life-stages (pupae, teneral adult, adult) which are highly susceptible to winter-kill (Reid 1962, 1963; Amman and Cole 1983). This delayed progression occurs when cooler temperatures in the fall slow development in the third- and fourth-instar larvae. Second, synchrony in development is accomplished when larvae from late-hatching eggs are able to catch up in development after temperatures are too cool for the later instars to develop. Development in third- and fourth-instar larvae halts in the cooler temperatures, but eggs and first- and second-instar larvae continue to develop due to lower developmental thresholds. Eventually, this catching up allows for coincident adult emergence. Temporally synchronized eclosion encourages *en masse* attack, thus enabling beetles to overcome the defenses of larger diameter host trees. Because larger diameter trees provide more food (phloem) for the

developing brood, coincident adult emergence eventually may lead to an epidemic population.

I tested the synchrony hypothesis using the developed phenology model driven by field recorded phloem temperatures. The model was initiated with a range of egg cohorts dispersed over several days to represent a wide oviposition distribution. If the thermal threshold hypothesis is valid, inherent temperature thresholds and flexibility in development of each life-stage should allow for eventual synchrony and coincident adult emergence as individuals pass through the life cycle. Phloem temperatures from both the north and south side of the bole were used to drive the model.

The model was initiated with three different recruitment levels of egg cohorts: (1) 100 eggs laid during 1 day; (2) 100 eggs laid over 10 days; and (3) 100 eggs laid over 20 days. A comparison of model-predicted results using phloem temperatures from the north side of the bole is shown in Figure 2.6. In larval instar I, the timing of development and eclosion among the three recruitment levels was widely dispersed, but less so by the time individuals reached larval instar II. After moulting to larval instar III, the individuals developing from eggs laid over a 20-day period were temporally synchronized with those developing from a single cohort (eggs laid on a single day), and entered the fourth-instar only a few days apart. A similar outcome occurred when phloem temperatures from the south side of the bole were used to drive the model. Although the warmer, southern exposure temperatures resulted in faster development in all instars, moulting to the fourth-instar was coincident. These results suggest that, in this temperature regime, the late hatching eggs catch up in the third larval instar. Although the proportion of individuals in each life-stage was altered, the ultimate timing of eclosion to the teneral adult was coincident, independent of the initial recruitment distribution. These observations imply that seasonality can serve to

synchronize phenology, and that inherent thermal thresholds may indeed be an important life-history strategy for the mountain pine beetle.

Conclusions

Phloem temperature measurements of infested lodgepole pine trees revealed the large amount of daily fluctuations and extreme temperatures to which mountain pine beetles are exposed. Constant temperature experiments provided a measure of the temperature-dependent development in the eggs, larval instars, and pupae. A phenology model was developed that uses both of these to simulate development of individual mountain pine beetles in the phloem of lodgepole pine trees. Results from this study indicate that mountain pine beetle life-stages have different thermal thresholds and developmental time functions that together tend to synchronize individuals of distinct cohorts for eventual coincident adult emergence. Because seasonal temperature cycles are universal, this life-history strategy may also be found in other insect species.

The ability to predict life-stage specific phenological development of mountain pine beetles in lodgepole pine has important applications for both management and research endeavors. This phenological model will help in our understanding of the interaction between beetle, stand, and at least one environmental factor, temperature, which influences population dynamics. As additional information of mortality and oviposition are included and field measurements for validation are obtained, the utility of the model as a component for mountain pine beetle management and population research will be increased.

Table 2.1. Functional forms of the developmental rate and distribution models used for describing mountain pine beetle phenology.

Developmental Rate Models

where:

R(T) = development rate at T
 T = temperature above T_{min}
 p_1, p_2, p_3, p_4 = parameters to be estimated for each model
 $\alpha = (p_3 - T) / p_4$

Logan TM1 (Logan et al. 1976):

$$R(T) = p_1(e^{p_2 T} - e^{p_2 \alpha})$$

Logan TM2 (Logan et al. 1976):

$$R(T) = p_1(1 + p_2 e^{-p_2 T})^{-1} e^{-\alpha}$$

Linear (Logan 1988):

$$R(T) = p_2(T - p_1)$$

Distribution Models

where:

F(t) = cumulative probability of complete development
 at normalized time t.
 p_1, p_2, p_3, p_4 = parameters to be estimated for each model

Logistic (Régnière 1984):

$$F(t) = [1 + e^{-p_1(t-1)}(.5^{-p_2} - 1)]^{-\frac{1}{p_2}}$$

Stinner (Stinner 1975):

$$F(t) = (1 - \beta)^\theta$$

where: $\beta = (p_1 - t) / (p_1 - p_2)$
 $\theta = p_3 \beta^{p_4}$

Weibull (Wagner et al. 1984):

$$F(t) = 1 - e^{-(t-p_1)/p_2}^{\theta}$$

Table 2.2. Estimated parameter values, adjusted r^2 , and sample sizes (N) for developmental rate and distribution models.

Lifestage	Developmental Rate Model	Distribution Model
Egg	Logan TM1 $p_1 = 0.029763$ $p_2 = 0.141571$ $p_3 = 22.51464$ $p_4 = 3.164244$ $N = 8$ $r^2 = 0.979$	Weibull $p_1 = 0.4933408$ $p_2 = 6.9159520$ $p_3 = 0.5411934$ $r^2 = 0.961$
Instar I	Logan TM2 $p_1 = 1.018901$ $p_2 = 72.24579$ $p_3 = 0.339336$ $p_4 = 24.22940$ $p_5 = 4.307345$ $N = 6$ $r^2 = 0.984$	Weibull $p_1 = 0.2071156$ $p_2 = 4.7405750$ $p_3 = 0.8722730$ $r^2 = 0.937$
Instar II	Logan TM2 $p_1 = 1.001610$ $p_2 = 36.70492$ $p_3 = 0.377676$ $p_4 = 18.33516$ $p_5 = 3.905421$ $N = 5$ $r^2 = na^*$	Weibull $p_1 = 0.0034052$ $p_2 = 2.2482860$ $p_3 = 1.2160780$ $r^2 = 0.861$
Instar III	Logan TM1 $p_1 = 0.078989$ $p_2 = 0.085548$ $p_3 = 13.04908$ $p_4 = 1.509073$ $N = 4$ $r^2 = na^*$	Logistic $p_1 = 8.138001$ $p_2 = 1.941817$ $r^2 = 0.853$
Instar IV	Linear $p_1 = 10.93365$ $p_2 = 0.010013$ $N = 3$ $r^2 = 0.951$	Stinner $p_1 = 0.388004$ $p_2 = 24.88443$ $p_3 = 0.562433$ $p_4 = 46.50753$ $r^2 = 0.743$
Pupae	Linear $p_1 = 13.09982$ $p_2 = 0.022251$ $N = 3$ $r^2 = 0.9847$	Logistic $p_1 = 36.42710$ $p_2 = 4.200781$ $r^2 = 0.747$

* Insufficient degrees of freedom for computation of r^2

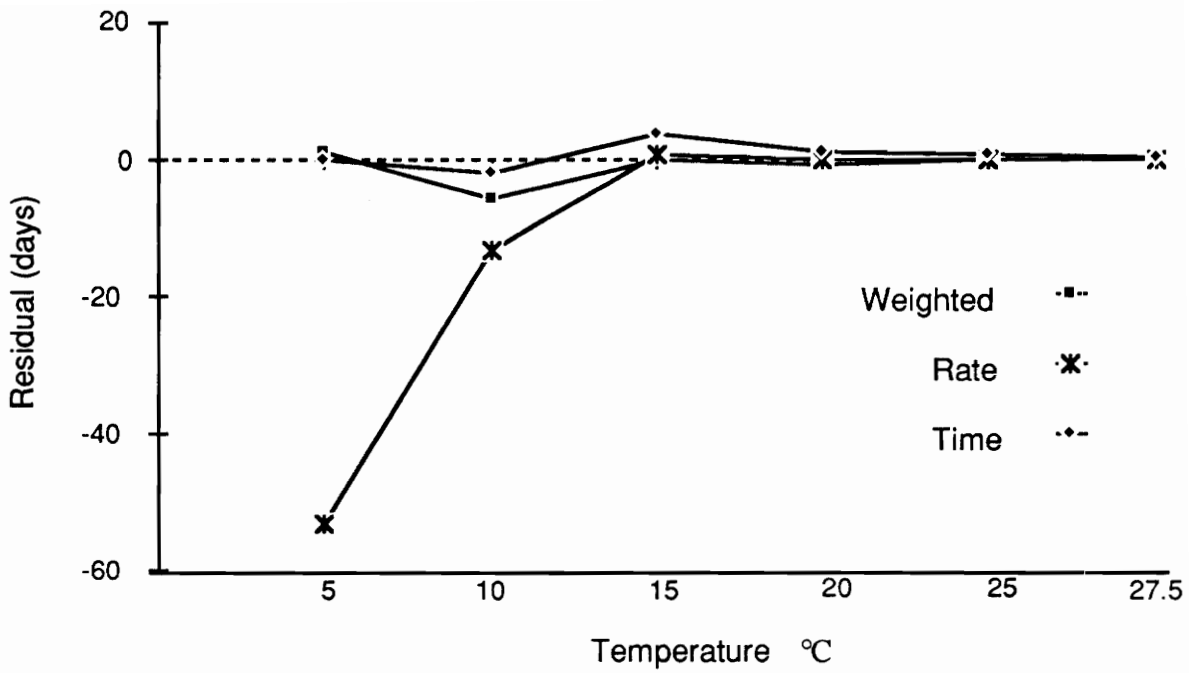


Figure 2.1. Residual values (observed days minus predicted days) using model TM2 (see Table 2.1) with observed time data, developmental rate data, and the least squares estimate weighted with $1/\text{rate}^2$.

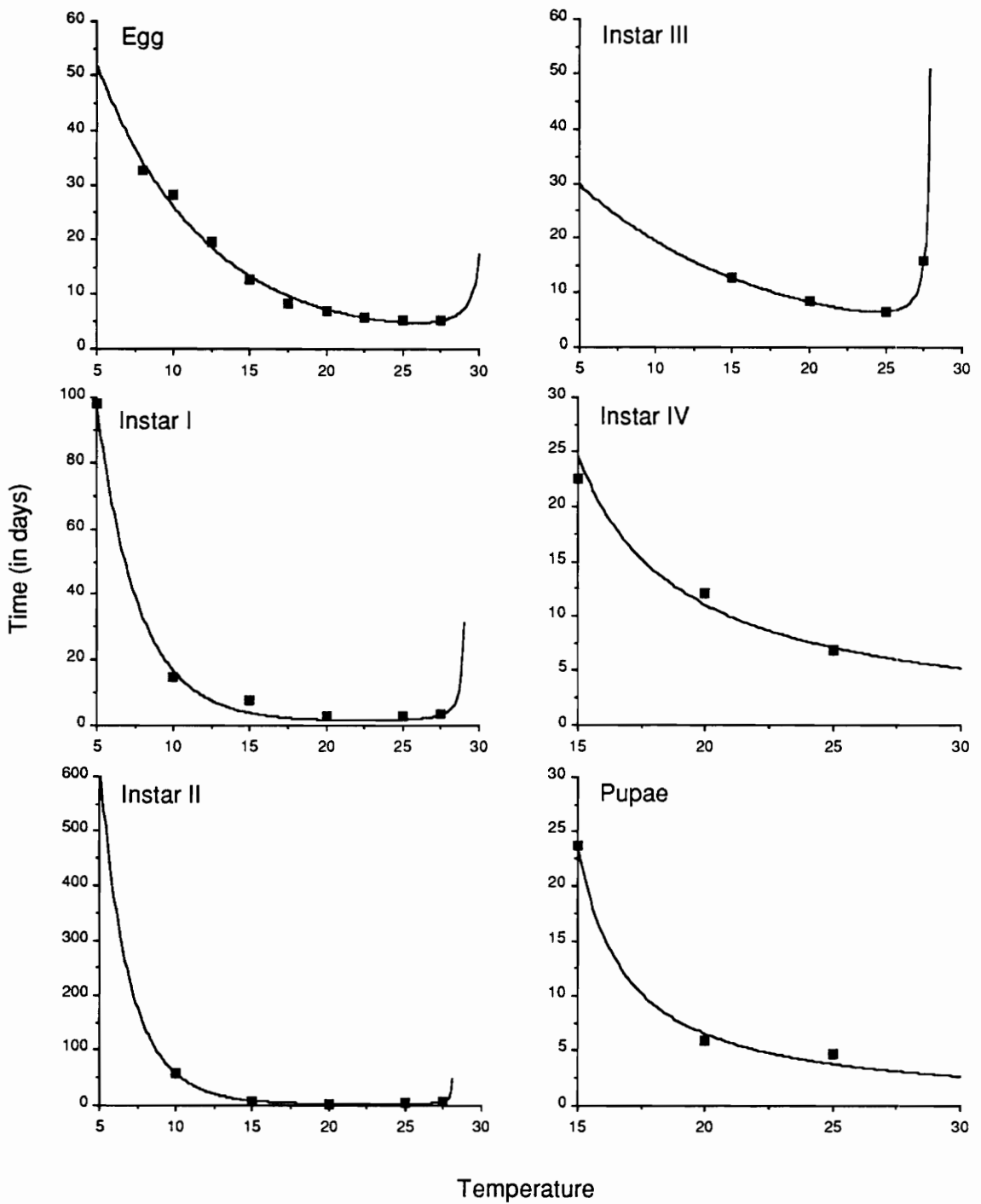


Figure 2.2 Developmental time functions for eggs, larval instars, and pupae fit to median times at constant temperatures. Equations and estimated parameters for developmental functions are in Tables 2.1 and 2.2. Curves represent the time (in days) to complete the life-stage at each constant temperature.

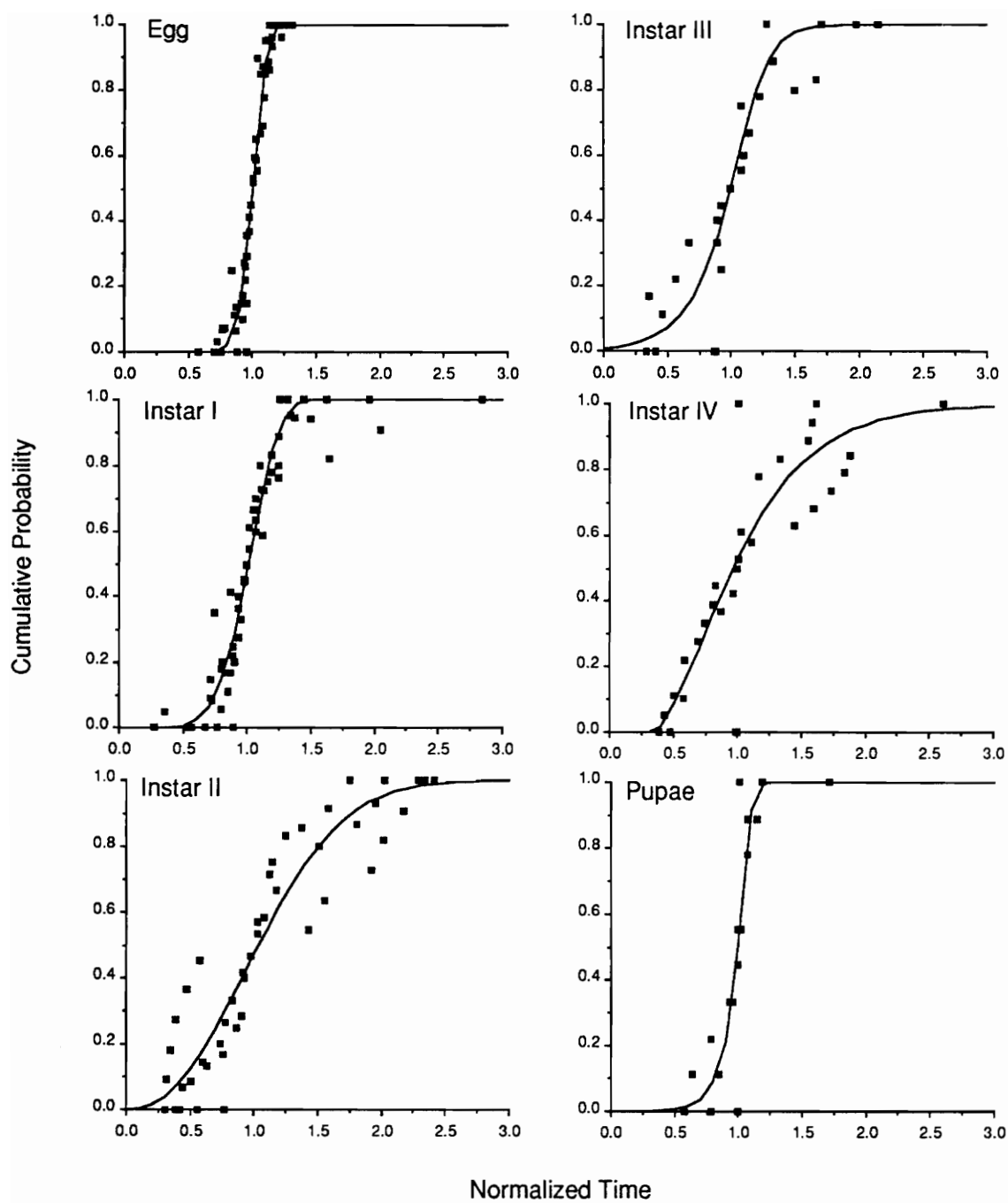


Figure 2.3. Predicted cumulative probability of emergence for eggs, laral instars and pupae compared to observed normalized values. Equations, estimated parameters, and sample sizes for distribution functions are in Tables 2.1 and 2.2.

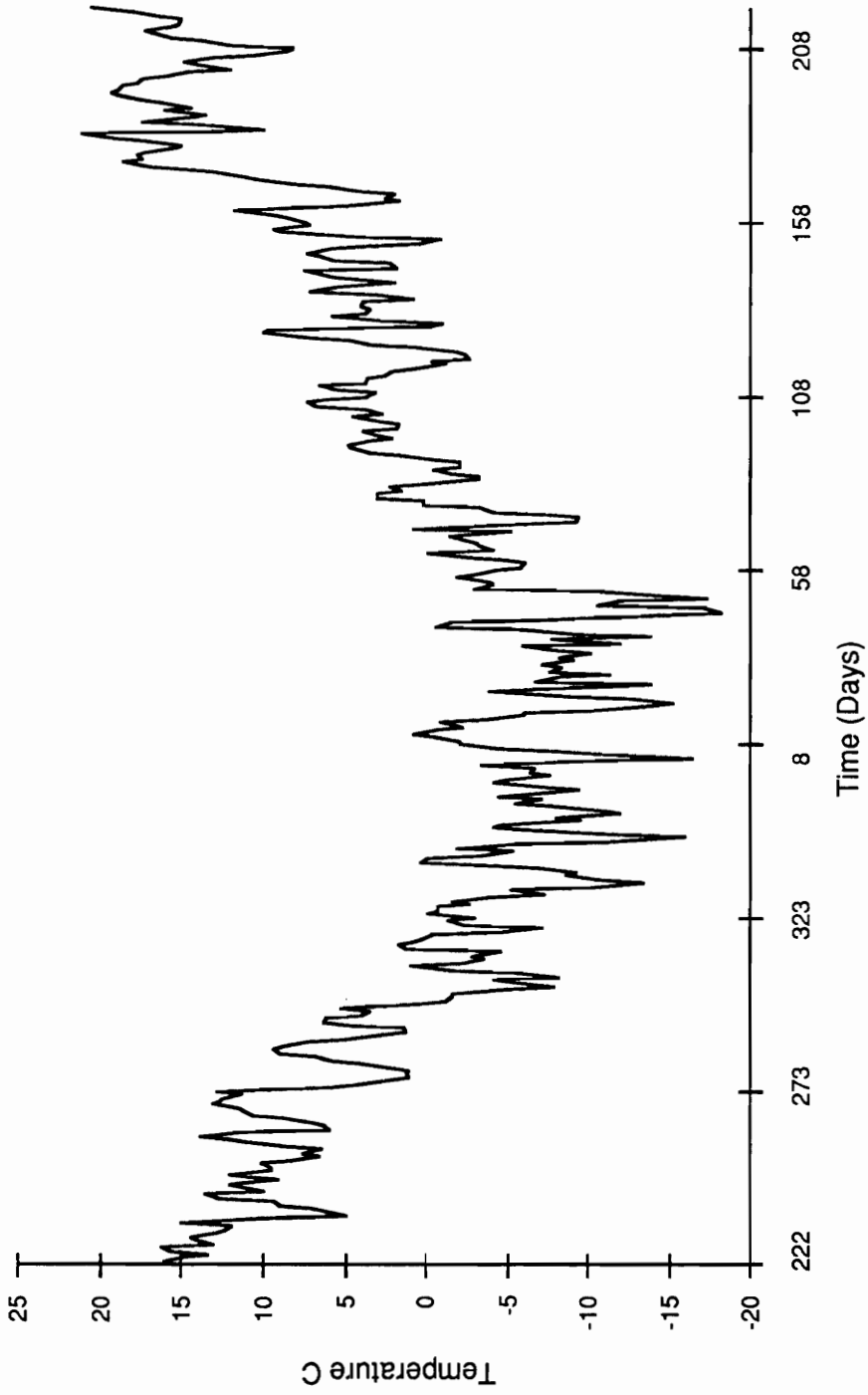


Figure 2.4. Average phloem temperatures measured on the north side of a 25.1 cm dbh lodgepole pine in the Sawtooth National Recreation Area, ID infested with mountain pine beetles.

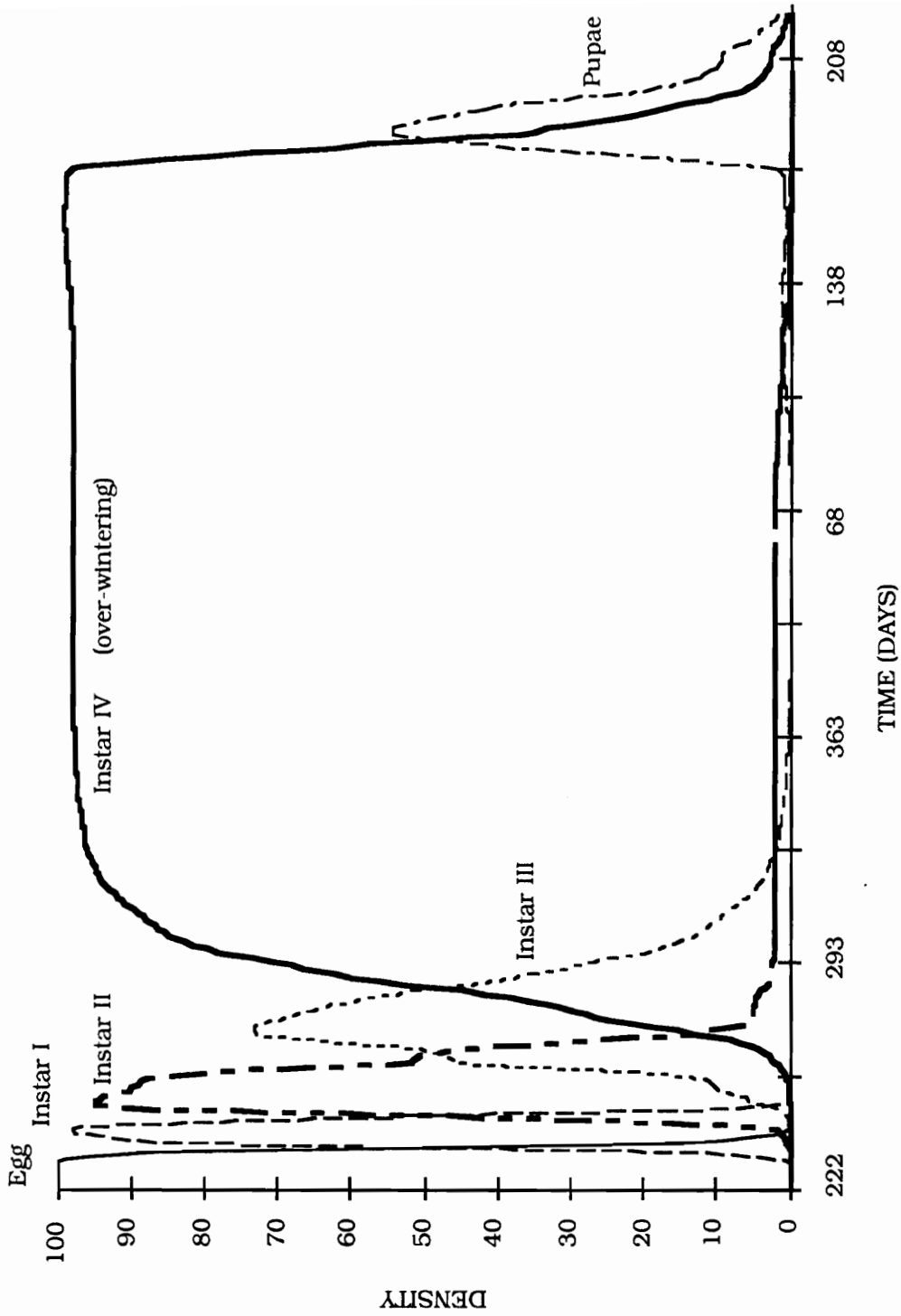
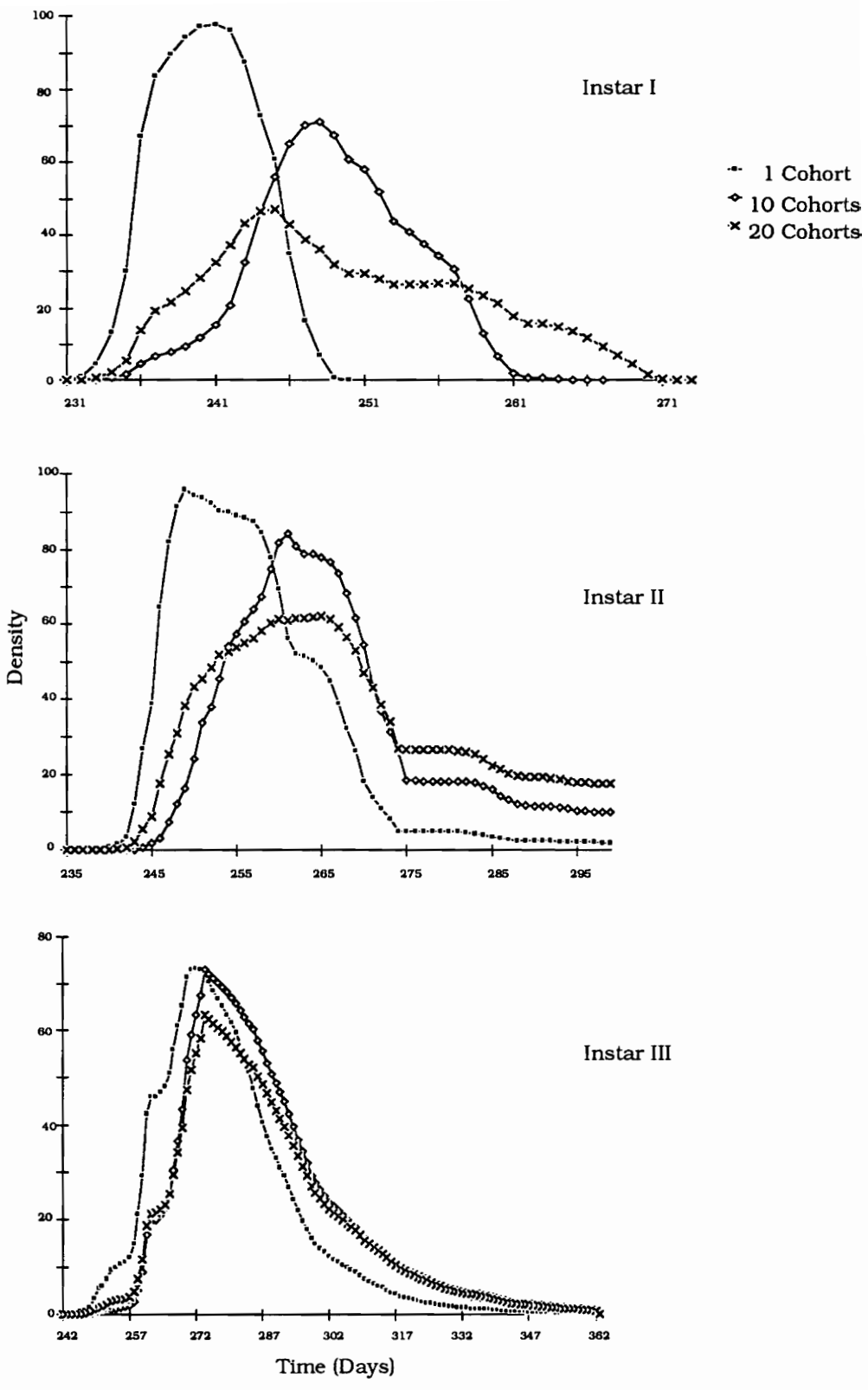


Figure 2.5. Density in each life-stage predicted by the phenology model using phloem temperatures from an infested lodgepole pine in the Sawtooth National Recreation Area, ID. The model was initiated with 100 eggs on day 222.

Figure 2.6. Density of larvae in Instar I, Instar II, and Instar III showing the temporal synchrony predicted by the simulation model. The phenology model was initiated on day 222 with 3 recruitment levels of egg cohorts: 1 cohort (100 eggs laid on a single day), 10 cohorts (100 eggs laid over 10 days), and 20 cohorts (100 eggs laid over 20 days). Note the difference in time scale between instars.



Chapter 3.

An Evaluation of Risk Classification Systems for the Mountain Pine Beetle in Northern Montana and Concepts for Improving Predictions

Introduction

Forest management requires knowledge of the biological and ecological factors which regulate forest ecosystem processes. Insects are an important component of these processes, and consequently, knowledge of insect pest population dynamics is fundamental to the long-term forest planning procedure. One aspect particularly important to management is an understanding of stand conditions which are most advantageous to insect pests, and therefore increase the likelihood that a stand will undergo an extensive infestation. This is especially important for insect pests, such as the mountain pine beetle (MPB) (*Dendroctonus ponderosae* Hopkins) where direct control measures are neither adequate nor feasible. Under optimal conditions, MPB populations can rapidly reach epidemic levels. Once an epidemic starts, control over wide areas is not possible, especially in pure lodgepole pine (*Pinus contorta* Douglas) (LPP) stands (McGregor 1978). Although the MPB is an important component of the LPP ecosystem and infestations may hasten the succession of the stand, an MPB outbreak often results in a reduction of economic benefits. The task currently facing forest managers is to lower the probability that a MPB population will reach epidemic levels. To do this, stands which have a high likelihood of sustaining epidemic level populations must be identified so that preventive measures can be applied in a timely manner. Hazard or risk rating methods which quantitatively describe the relationship

between insect pest populations and forest stand conditions have often been used for this task.

Hazard and risk systems are tools used by forest managers to predict future insect activity relative to the location of a forest stand, and conditions within the stand (Hicks et al. 1987). Historically, in forest insect management, the terms hazard and risk have been used in a variety of ways. In most instances hazard and risk were used interchangeably, even within the same sentence. Other terms such as vulnerability and susceptibility have also been used to describe particular aspects of rating systems. For example, the likelihood of defoliation by the gypsy moth (*Lymantria dispar* L.) is susceptibility, whereas the probability of damage is vulnerability (Hicks 1990). For this pest, the term hazard includes information about land management objectives, and risk is the term used for a final assessment combining hazard, vulnerability, and susceptibility (Ravlin et al. 1990). Both hazard and risk have also been used to describe systems which identify stands susceptible to the southern pine beetle (see Hertel 1981).

A variety of classification methods, defined as both hazard rating and risk rating, have been developed for the MPB as well. Because an MPB infestation usually results in death of the host tree, all these methods related hazard or risk to tree mortality in some manner. Some systems were based on regional-level descriptions, such as a historic map depicting the frequency and intensity of MPB infestations (Crookston et al. 1977), and climate related parameters (Safranyik et al. 1975). Other systems were based on stand and host tree characteristics including indices of stand competition (Schenk et al. 1980, Anhold and Jenkins 1987), tree age, diameter, and climatic zone (Amman et al. 1977), host tree growth and vigor (Mahoney 1978, Waring and Pitman 1980), tree physiological maturity (Shrimpton and Thompson 1981), and a

combination of several of these factors (Berryman 1978, Stuart 1984). In most instances, these systems were developed to provide a predictor of either stand *susceptibility* or stand *resistance* to MPB populations. In general, *susceptibility* was defined as either the likelihood of an MPB outbreak occurring in a given stand, or the ability of the stand to generate and sustain a large beetle population. Stand *resistance*, on the other hand, was defined as the ability of the average dominant or codominant lodgepole pine in a stand to defend itself against an MPB attack (Berryman 1978). Unfortunately, the melange of terminology has resulted in confusion over what is meant by a particular method and how it should be interpreted.

The objective of this chapter is to evaluate several of the current MPB hazard and risk rating methods. Shore et al. (1989) tested the systems using data collected in lodgepole stands in British Columbia. Preliminary results from their study indicated that none of the methods adequately described the MPB/LPP relationship in a manner that could be used for predictive purposes in British Columbia. The relationships these systems are based on were also tested in lodgepole pine stands in Southeastern Wyoming, and were found unsuitable or in need of modification (Katovich and Lavigne 1985). These methods will be evaluated using data from three forests in northern Montana to see if geographic region has a bearing on the performance of the rating systems. The purpose of this evaluation is to determine how well each method predicts MPB caused mortality in these forests. Using information gained from these methods, an additional model for rating the susceptibility of lodgepole pine stands to MPB populations will be explored. Finally, after reviewing the hazard and risk terminology as it is currently used in the systems being evaluated, I will discuss some new concepts and definitions for use in MPB risk rating. For now, the hazard and risk systems evaluated in the next section will be grouped under the general heading Risk

Classification Methods, and each will be described using the original terminology of the authors who developed the particular method.

Evaluation of Mountain Pine Beetle Risk Classification Methods

Four systems, or at least the concepts the systems were based on, were evaluated in this study: Amman et al. (1977), Mahoney (1978), Schenk et al. (1980) and Berryman (1978). I will give a brief description of each method, but for further detail the reader is directed to the original publications. Each of these methods were originally developed to predict the risk or hazard rating of a stand to an MPB infestation. Risk and hazard were defined differently in each method, although both terms were always related to the mortality incurred in a stand. Mortality thresholds were a function of the particular rating method. Evaluations were performed by using the methodology described in each system to predict the risk (or hazard) rating for each stand in the data set described in the next section. The predicted results were then compared to the actual mortality observed in each stand.

Data Description

As part of the Canada/United States Mountain Pine Beetle program, 105 stands on the Lolo, Kootenai, and Flathead National Forests were surveyed during the summer of 1984. Only those stands in areas of climatic suitability to an MPB infestation were included in the study (see Amman and Anhold 1989 for a description of the study). The level of MPB infestation in the survey stands ranged from no recent infestation to completion of an outbreak. Only stands with at least 75 percent lodgepole pine were included in the study. Each stand was sampled using a 10-BAF (basal area factor in

square feet per acre) variable radius plot cruising method for ten plots located on a 100 meter square grid. This data set was used to evaluate the risk classification methods.

Final surveys are being conducted to determine the cumulative mortality in each stand. In each Forest the MPB population trend was categorized as increasing, declining, or static by comparing the trees per acre infested the year of the study to the trees per acre infested the previous year. For example, if the trees per acre infested the previous year were greater than the current year, the MPB population trend was assumed to be declining. Preliminary graphical analysis revealed that on the Flathead National Forest the relationship between the percent trees per acre infested and at least one explanatory variable, crown competition factor (CCF), seemed to differ by population trend (Fig. 3.1). Therefore, only those stands from the initial survey which had a static or declining infestation were used so that all stands being analyzed had experienced similar infestation phases. Trees coded as killed by MPB were included in density calculations to represent the stand structure before the beetle entered the stand. Cumulative mortality included all trees killed by the MPB in the 5 years previous to the survey. Stands with no infested trees were included in the analysis to provide a statistical comparison between infestation occurrence and non-occurrence. Figure 3.2 provides an indication of the cumulative and yearly mortality in each Forest analyzed, and descriptive statistics for the initial year are in Table 3.1.

Results

The system developed by Amman et al. (1977) includes measures of climatic suitability (latitude and elevation), and tree characteristics (age and diameter at breast height (dbh)). In this method, hazard is the expected mortality in a stand as measured by the percent infested trees. Amman rated these 4 variables on a scale of 1-3

according to established thresholds. For each stand, the ratings for the 4 variables are multiplied to obtain a single value for the stand which represents the expected mortality (and subsequent hazard): 1-9 low hazard (< 25% infested trees), 10-18 moderate hazard (25-50% infested trees) and 27 high hazard (> 50% mortality). Only validation data for part of the stands on the Kootenai and Flathead Forests had the required variables necessary for evaluating this method. Of the 48 stands evaluated, only 1 was predicted to have a low hazard using Amman's system, although 73% of the stands were observed to have < 25% mortality, which is indicative of low hazard (Table 3.2). 65% of the stands were predicted as moderate hazard, although only 21% were observed in that category. 26% of the moderate hazard stands were correctly categorized, but less than 1% of the stands with predicted high mortality actually experienced high mortality. Overall, only 18.75% (9 stands) were correctly categorized. Since most of the error occurred when low hazard stands were rated as moderate, predictions from this system tend to be more conservative.

In the Mahoney (1978) system, many terms including susceptibility, resistance, and risk are used. Mortality is expressed as the proportion dead LPP in the stand due to the MPB. This method is based on the periodic growth ratio (PGR):

$$\text{PGR} = \text{current 5 year radial increment} / \text{previous 5 year radial increment.}$$

A stand PGR average < 1.0 indicates a decline of overall stand vigor and subsequent susceptibility to an MPB infestation, whereas a PGR \geq 1.0 suggests that on the average the stand is relatively vigorous and should be resistant to MPB attacks. Thus, based on this theory, Mahoney assumed that a stand with a PGR < 1.0 should have greater tree mortality due to the MPB. Not all stands in the validation data set had the

required data to evaluate this system. Of the stands tested, 71% of the observed stands experienced < 10% mortality, although using the PGR method 50% mortality was predicted in each category (Table 3.3). Overall, slightly more than 50% of the stands were correctly rated using this method.

Schenk et al. (1980) based their system on the hypothesis that stand susceptibility (and subsequent hazard) is a function of average stand vigor and the availability of food. Crown competition factor (CCF) (Krajicek et al. 1961, Wycoff et al. 1982) is used as a measure of competitive stress (vigor), and the proportion of stand basal area made up of lodgepole pine (%BALP) as an indication of the food availability. The interaction between these variables provide a stand hazard rating index (SHR):

$$\text{SHR} = \text{CCF} * \% \text{BALP} / 100.$$

SHR is an indication of the percentage of lodgepole pine basal area which will be killed by the beetle (%LPBAK). Although Schenk et al. originally found SHR to increase with increasing CCF and %LPBAK, Shore et al. (1989) and McGregor et al. (1981) observed that SHR was inversely related to %LPBAK, as was CCF. Similar findings were observed in this study (Figs. 3.3 and 3.4). Therefore the regression models developed by Schenk et al. were not considered useful for rating stands in this study.

Berryman (1978) developed a model for predicting the risk or hazard of a stand to an MPB outbreak, thereby equating the terms risk and hazard. In this model, Berryman proposed that phloem thickness, climatic suitability and host resistance were three variables necessary to adequately describe the interaction between lodgepole pine and MPB. These variables were combined using the ratio of PGR to SHR as a measure of a average host resistance, and percent of the lodgepole pine basal area with

a phloem thickness $> .10$ inches as a measure the intensity of the beetle infestation. Of those stands in the validation data set, most had an average phloem thickness less than $.10$ inch and this variable could not be evaluated. Based on model assumptions, mortality in the stand (%LPBAK) should decrease with increasing stand resistance. There was a slight trend in this direction (Fig. 3.5). Three stands with resistance values greater than 1.3 experienced less than 10% mortality. There were no other observable trends in %LPBAK as predicted by resistance (PGR/SHR).

Discussion

Of the relationships evaluated, SHR and CCF exhibited the strongest association with lodgepole pine mortality. The relationship between CCF and %LPBAK is similar to the relationship between mortality and stand density index (SDI) described by Anhold and Jenkins (1987). Both CCF and SDI take into account the size of the trees in the stand. SDI uses average quadratic mean diameter (QMD), while CCF uses the trees per acre represented by each tree. Beetle-caused mortality decreased in stands with $CCF > 200$ (Fig. 3.3). Anhold and Jenkins (1987) observed a similar density threshold using SDI. Extremely dense stands are less favorable to MPB populations due to thinner phloem in the crowded conditions. In stands with lower CCF values however, mortality was high. Because closed canopy conditions, and subsequent competition, begin as CCF approaches 100 (Krajicek et al. 1961), the trees may be stressed just enough to provide conditions conducive to MPB attack, yet still have phloem thickness to support the population.

The characteristics used in the Amman et al. (1977) system provide a good indication of the climatic regions favorable to MPB population growth, but do not provide enough detail specific to a particular stand to differentiate between low,

moderate, or highly susceptible stands. Additionally, only those stands within the zone of climatic suitability to MPB populations were included in this study, discounting the effect of climate.

Mahoney's system is based on the assumption that vigorous stands will be resistant to MPB infestations. This assumption, however, is dependent upon the number of beetles in the area. Stands with increased vigor will usually have a higher proportion of thicker phloem trees. Because phloem is the food of developing brood, these stands will also be favored by beetle populations and provide optimal conditions for increases in population size (Amman 1972, Cole, D.M. 1973). Therefore, although endemic populations usually will not start in highly vigorous stands, these stand types provide optimal conditions for rapid population growth. Additionally, there are situations where PGR values > 1.0 are not necessarily indicative of resistance to MPB attacks. For example, in periods of drought and in stands where MPB mortality has recently occurred (Amman 1983), PGR values may be > 1.0 . Also, growth in radial increment tends to decline after about 30 years (Shrimpton and Thompson 1981). Therefore, on the average, after a tree reaches 30 years, PGR may be less than 1.0 despite the resistance capabilities of the trees.

Stuart (1984) suggested that stand hazard ratings should include both vigor and tree size, and Amman and Anhold (1989) suggest tree size and stand density. The methods evaluated included these factors, as well as others, yet only Berryman's system attempted to put them all together. None of the methods evaluated provided adequate estimates of stand susceptibility (measured as percent LPP mortality) on the Lolo, Flathead or Kootenai Forests. Shore et al. (1989) observed similar results in British Columbia. Because the relationship between lodgepole pine and the mountain pine beetle is a complex interaction of both host and beetle population attributes, more

than a few variables will be necessary to describe the association. In an attempt to determine which of the identified factors have the greatest influence on the amount of MPB caused mortality, additional combinations of variables were examined using a logistic regression model.

A Logistic Model for Mountain Pine Beetle Risk Classification

Methods

Evaluation of the available methods for MPB risk classification provided a summary of variables that describe important correlative aspects of the relationship between MPB populations and lodgepole pine. Based on these and previous studies, combinations of 16 variables were analyzed for their utility in describing the association between lodgepole pine and MPB caused mortality. The variables included total stand basal area (BA), lodgepole pine BA (LPBA), trees per acre (TPA), trees per acre lodgepole pine (LPTPA), stand density index (SDI), lodgepole pine SDI (LPSDI), quadratic mean diameter (QMD), lodgepole pine QMD (LPQMD), average dbh (DBH), percent lodgepole pine > 8.5" dbh (%BIGLP), percent lodgepole pine between 5.0" and 6.9" (%SMLP), percent of the basal area in lodgepole pine (%BALP), average phloem thickness (PHLOEM), crown competition factor (CCF), elevation, and habitat. Habitat types were grouped according to vegetation management guidelines on the Flathead National Forest (Table 3.4). These groups were included in the regression as indicator variables (Zar 1984). HAB1 = Groups 2, 3, and 4, HAB2 = Group 5, and Group 6 is included in the intercept term of the regression model. Each forest, Flathead, Lolo, and Kootenai, was also included in the analysis as an indicator variable, ID1 = Flathead, and ID2 = Lolo.

Logistic regression was used to describe the relationship between stand characteristics and the likelihood of an infestation. The likelihood of an infestation was represented as the proportion trees per acre lodgepole pine infested. Logistic regression is based on the cumulative logistic probability function:

$$P_i = F(\alpha + \beta X_i) = \frac{e^{\alpha + \beta X_i}}{1 + e^{\alpha + \beta X_i}}$$

where:

$$\beta X_i = X_{i1} * \beta_1 + X_{i2} * \beta_2 + \dots X_{ip} * \beta_p$$

α = intercept parameter

$\beta = \{\beta_1, \dots, \beta_p\}$ is a vector of regression parameters for p independent variables

$X_{i1}, X_{i2}, \dots, X_{ip}$ is a vector of independent variables for the ith observation

P_i is the probability of the ith stand being infested, measured as the percent trees per acre infested

Logistic regression was picked for several reasons. Predicted probabilities (P_i) are bounded between 0 and 1 as $\alpha + \beta X_i$ increases from $-\infty$ to $+\infty$, thereby providing a more meaningful estimate than results from a typical regression model which are unbounded (Wrigley 1985). Logistic regression provides a continuous measure of the probability of the pest event occurring, instead of a simple classification of low, moderate or high. The method of maximum likelihood, was used to estimate parameters for the model. Maximum likelihood estimates were computed using

iteratively reweighted least squares, where the weights were the reciprocals of the variances (Procedure NLIN, SAS Institute 1988).

Backward stepwise selection ($\alpha = .10$) was initially used to identify which of the original explanatory variables were most valuable in describing an MPB infestation. Collinearity among the variables was reduced by eliminating redundant and highly correlated variables. It has been hypothesized that using actual plot values for calculating mensurational measurements, rather than averaging them over a stand, helps describe the variation within the stand (Pukkala 1990). Additionally, using stand density values calculated at the plot level may better describe microclimatic conditions within the stand. For example, a plot with few trees per acre will be more open and thus sunnier than a plot which has the shading effect of a large number of trees per acre. These microclimatic effects are thought to be an important part of MPB survival (Bartos and Amman 1989). Therefore, separate analysis were performed: 1) using individual plot data to calculate density measures used as explanatory variables, and 2) using a stand average for calculating density measures. The alternative models developed using different combinations of the explanatory variables were compared using r^2 and F ratio statistics from the regression analysis.

Results

From the regression analysis and goodness of fit statistics, it was determined that TPA, LPQMD and %BALP provided the best model when plot densities were used. However, the statistical fit ($r^2 = .349$) and results graphically depicted were poor (Fig. 3.6). The explanatory variables apparently were not adequate for describing the variation between similar plots and the high mortality which occurred in a single plot.

When plot density values were averaged for a stand, a better fit was obtained as described below.

Using stand-level data for all the forests, stand density (CCF), food availability (%BALP and LPQMD), site suitability (HAB1 and HAB2), the forest indicator variables (ID1, ID2), and two interaction terms (ID1 * %BALP, and ID2 * %BALP) were the most significant (Table 3.5). The significance of the stand indicator variables implies that there are factors associated with each forest that may help to explain tree mortality. Determining these factors and including them in the model could increase the predictive ability. However, the current inclusion of the indicator variables as stand delineators limits the generality of the model. Standardized residual plots

$$\frac{(observed-predicted)}{\sqrt{predicted(1-predicted)}}$$

for each explanatory variable are in Appendix I. There was no observable trend in model residuals due to these variables. With the exception of one stand, predictions for stands in the Lolo National Forest were slightly more accurate than predictions for stands on the Flathead and Kootenai National Forests (Fig. 3.7). Using the logistic model, predicted percent trees per acre lodgepole pine infested were in general less than observed as depicted by the standardized residuals of observed and predicted percent trees per acre infested (Fig. 3.7).

Discussion

Although many variables have been found to be associated with beetle caused mortality, general predictions from 4 methods which use these associations were found to be unsatisfactory for stands in three Forests in northern Montana. A logistic

regression model developed using a more complex combination of variables describing stand conditions was also found to be inadequate for predicting percent trees per acre infested. Why have none of these methods proven to be useful? Obviously, many important factors are not included by simply measuring trees in a stand. I will discuss this question and attempt to clarify terminology used in risk classification for the MPB in LPP stands.

Biological systems in nature contain unknown and random elements which are difficult to explain. For example, in almost every forest where an MPB epidemic occurs, it is possible to find an area with apparently identical conditions and no outbreak during a specified interval of time. A risk rating system ideally attempts to predict the relative frequency of this event (Stage and Hamilton 1981). For the MPB however, risk rating should not entail merely predicting the occurrence of an MPB population. Endemic MPB populations are ubiquitous in LPP stands. Additionally, there are two separate events in the dynamic relationship between MPB and unmanaged LPP stands which should be predicted. The two phases are separated by an unstable outbreak threshold which divides the MPB/LPP system into two behavioral domains (Berryman 1982). The first requiring prediction is the likelihood that an endemic population will abruptly increase to epidemic densities in a particular stand, and the second, if stand and site conditions are sufficient to sustain the increased numbers of beetles (Fig. 3.8). The first requires knowledge of endemic populations, and the second epidemic population behavior.

Traditionally, MPB risk classification systems have attempted to address both processes, although the distinction between the two events was not emphasized. Indices of stand resistance, such as PGR, are important for measuring conditions that will initiate an outbreak or increase the likelihood of transition from the endemic to

epidemic phase. On the other hand, site and stand characteristics such as age, diameter and stand density provide an indication of stand susceptibility, the ability of a stand to sustain an epidemic beetle population. Weather and the beetle population size are important factors in both events. Once the population has reached the epidemic level, even resistant trees may be attacked and consequently, host resistance is not as important at this stage.

Many catalysts are thought to precipitate the transition from the endemic to epidemic MPB population phase. A reduction in tree vigor (resistance) caused by secondary associated beetles, diseases, drought, and competition is an important factor (Schmitz 1988, Tkacz and Schmitz 1986, Berryman 1976, Beal 1934). Weather, an uncontrollable event which can not be predicted, is also an important factor in determining population survival, both during brood development and the colonizing flight period (Safranyik 1978, Chapter 2). How the many causal factors interact to cause the transition from an endemic to epidemic population is still unclear. Additionally, stress factors which reduce stand vigor and weaken a tree are difficult to measure, and are not included in routine stand surveys. Tree resistance (vigor) itself varies within a year (Shrimpton and Reid 1973), and accurate predictions by any means are difficult. Consequently, the ability to measure the likelihood of an abrupt population increase and subsequent transition from the endemic to epidemic phase is limited. This was illustrated in the evaluation of Mahoney's system based on PGR, a measure of tree vigor. Predictions from this system were no better than those expected due to chance in a 2 category analysis (Table 3.2).

Because the MPB is an eruptive pest, once an outbreak starts it will normally spread to adjacent stands as the increase in population size overwhelms host tree defenses (Berryman and Stark 1985). Therefore, the probability that a stand will

experience an MPB outbreak is dependent upon population density as well as site and stand conditions. Highly susceptible stands (based on site and stand conditions) can exist with little or no infestations if MPB numbers in the area are low. Conversely, highly resistant trees will be attacked if MPB population size in the surrounding area is high. Consequently, a measure of the beetle population in the vicinity should be included in a risk rating system (Paine et al. 1984, Shore et al. 1989).

None of the methods evaluated included a direct measure of the beetle population. Shore and Safranyik (pers. comm.) are currently developing a system which does take into account a measure of the surrounding population level. They describe a risk rating system for MPB which includes two levels: stand susceptibility, defined as a measure of the stand conditions predisposing to the *occurrence* and *growth* of an MPB population, and risk, the association of stand susceptibility and beetle population level. As mentioned, however, MPB populations are ubiquitous, and predicting the *occurrence* or presence of an endemic population is difficult. Additionally, the two distinct processes in the evolution of an outbreak population should not be combined. Susceptibility is an appropriate measure of the ability of a stand to sustain an epidemic population, but the transition, or *growth*, from an endemic to epidemic population is a distinct process and should be separate.

From this discussion, I envision 4 steps which should be considered in the forest management process of stands within the climatic zone of MPB populations: 1) identify conditions that increase the probability of an endemic population erupting to the epidemic population level (based on stand resistance factors), 2) identify site and stand conditions which will sustain an epidemic population (**susceptibility**), 3) determine the likelihood of an outbreak MPB population in a stand (during a specified time period) using stand susceptibility and MPB population pressure (**risk**), and 4)

determine the severity of the event, in terms of the amount of timber loss to expect once an MPB epidemic is initiated in a particular stand. Unfortunately, as mentioned, the mechanism which triggers an epidemic population is still unclear, and we are unable to accurately predict this phenomena (step 1). Factors which influence the ability of a stand to sustain an epidemic population (susceptibility) are known, however, and can be measured (step 2). Several causal factors including measures of stand density, food availability and tree size (see Table 3.6) were identified in this analysis and the alternative methods evaluated in this study.

Based on our current understanding of MPB behavior, the severity of the event (expected loss in a stand due to the beetle) (step 4) may be described using the same characteristics as are used for describing the susceptibility of the stand. Both relate to the ability of a stand to sustain an epidemic population. Cole, W.E. and McGregor (1983) developed a model which predicts the beetle caused loss expected in a stand over a 10 year period. Because the model may be initiated with beetle population numbers, it provides a method for evaluating both the *susceptibility* and *risk* of a stand which also includes MPB population level (step 3). In this manner, step 3 and 4 are combined into one model. Although validation of the Cole and McGregor model has revealed that it is inadequate in some Forests, silviculturists on the Flathead National Forest currently use it, rather than a "hazard rating" model, for prioritizing stands for harvest. Development of a similar simulation model which includes an indirect measure of MPB population size as a time-lagged variable and describes probability of infestation and an estimate of the loss expected will be described in Chapter 4. This type of model may well provide us with the best answers available until we gain a further understanding of endemic MPB dynamics in LPP stands.

Conclusions

A risk rating system for the MPB is not intended to be a panacea, but a guideline to help managers in the forest planning process. As noted by Mawby et al. (1989), acknowledgment of the different phases in bark beetle dynamics is important to consider when making stand management decisions. There are two distinct phases in the MPB/LPP system. The concepts important in describing population transition from the endemic to epidemic phase are different from those necessary to measure the ability of a stand to sustain a large MPB population (Fig. 3.8). Until biological/ecological knowledge concerning the former is unraveled, risk rating systems for MPB will provide the best information to a manager if they provide an estimate of stand susceptibility, risk, and subsequent loss. I have defined susceptibility as the ability of stand to support an epidemic MPB population, and risk is the likelihood of an outbreak population occurring in a stand. Risk includes a measure of the MPB population pressure as well as stand susceptibility. By combining these two factors into a measure of the expected loss in a stand it will allow managers to prioritize their available resources for treatment.

Use of a system by forest managers will be expedited if the only required information is that which is already available from routine stand surveys. One exception is the need for a measure of the MPB population in the area. Routine surveys for monitoring MPB population levels need to be implemented if risk rating systems are to be useful at the stand level. New technologies, such as geographic information systems, will help in this process. Because the variables used to measure the relationship between the MPB and stand mortality may differ by region and forest, systems should be tested adequately before using in an area other than where the model was developed.

Table 3.1. Descriptive statistics for data used to evaluate the risk classification methods. This data set was also used to estimate parameters for the logistic regression model. The data includes only those stands with a static or declining MPB population trend (see text).

Variable	Mean	Standard Deviation	Std. error of Mean
Flathead National Forest N = 45 stands			
TPA	413.02	109.04	16.25
LPTPA	310.60	142.82	21.29
BA	162.04	36.74	5.48
LPBA	115.64	39.21	5.84
CCF	213.93	43.80	6.53
LPQMD	8.63	1.44	.21
%LPBA	72%	.22	.03
QMD	8.60	1.18	.18
Kootenai National Forest N = 14 stands			
TPA	306.00	101.17	27.04
LPTPA	217.57	122.59	32.76
BA	156.00	30.23	8.08
LPBA	105.57	42.03	11.23
CCF	181.57	37.52	10.03
LPQMD	9.94	2.03	.54
%LPBA	67%	.21	.06
QMD	9.97	1.89	.50
Lolo National Forest N = 25 stands			
TPA	458.76	90.95	18.19
LPTPA	356.04	119.95	23.97
BA	135.60	32.72	6.42
LPBA	93.72	28.66	5.73
CCF	175.48	30.97	6.19
LPQMD	7.04	.79	.15
%LPBA	71%	.19	.04
QMD	7.36	.83	.17

Table 3.2. Comparison of observed and predicted results from Amman et al. (1977) system. Low = < 25% mortality, Moderate = 25-50% mortality, and High = > 50% mortality. Mortality is interpreted as the percentage of dead LPP in the stand. Observed and predicted count and share are the frequency and percentage of stands in each category. Proportion successfully predicted is the proportion of stands predicted to be in a certain category which were observed in that category.

		Predicted			Obs. Count	Obs. Share
		Low < 25%	Moderate 25-50%	High > 50%		
Observed	Low	1	22	12	35	.73
	Moderate	0	7	3	10	.21
	High	0	2	1	3	.06
	Pred. Count	1	31	16	48	1.0
	Pred. Share	.02	.65	.33	1.0	
	Proportion Successfully Predicted	1.0	.26	.06	Total = 18.75% Successfully Predicted	

Table 3.3. Comparison of observed and predicted results from Mahoney (1978) system. PGR ≥ 1.0 indicates mortality $\geq 10\%$, and PGR < 1.0 indicates mortality $< 10\%$. Mortality is measured as percent lodgepole pine infested.

		Predicted			
		$\geq 10\%$	$< 10\%$	Obs. Count	Obs. Share
Observed	$\geq 10\%$	4	3	7	.29
	$< 10\%$	8	9	17	.71
	Pred. Count	12	12	24	1.0
	Pred. Share	.50	.50	1.0	
	Proportion Successfully Predicted	.33	.75	Total = 54.1% Successfully Predicted	

Table 3.4. Habitat type groupings used for determining indicator variables in the regression analysis. Listed for each group are the abbreviations and codes, in parenthesis, for each habitat type in that group. Groupings are based on Vegetation Management Guidelines in the Forest Management Plan, Flathead National Forest.

Group 2:
DF/Caru-Aruv (322), DF/Caru (320), DF/Vacu (250)
Group 3:
DF/Vagl (280), GF/Xete (510)
Group 4:
AF/Libo-Vasc (663), AF/Xete-Vasc (692), AF/Vasc-Caru (731), AF/Xete (690)
Group 5:
WH/Clun-Clun (571), C/Clun-Clun (531), DF/Libo-Caru (292), WH/Clun (570), DF/Libo (290), GF/Libo-Libo (591)
Group 6:
AF/Clun-Xete (624), AF/Clun (620), AF/Alsi (740), AF/Libo (660), AF/Clun-Arnu (622), AF/Clun-Vaca (623), AF/Clun-Mefe (625)

Table 3.5. Parameter estimates and goodness of fit statistics for logistic regression model. Data used to estimate parameters is described in Table 3.1. CCF = crown competition factor, LPQMD = lodgepole pine quadratic mean diameter, HAB1 and HAB2 = habitat indicator variables, %BALP = percent of the basal area in lodgepole pine, ID1 and ID2 = stand indicator variables.

Variable	Estimate	Standard Error
Intercept	3.3857	1.6294
CCF	-.0129	.0043
LPQMD	.1676	.1207
HAB1	.7366	.3355
HAB2	.9221	.5324
%BALP	-6.0950	1.1952
ID1	-4.7279	1.2569
ID2	-6.0936	1.6154
ID1 * %BALP	5.2511	1.6271
ID2 * %BALP	7.9706	2.0136

N = 84 $r^2 = .82$ $F_{10,74} = 11.72$ $p < .001$

Table 3.6. Stand and site variables identified to be associated with mountain pine beetle caused lodgepole pine mortality. Variables are categorized by the systems in which each is used.

	Amman et al. (1977)	Mahoney (1978)	Berryman (1978)	Schenk et al. (1980)	Logistic Regression
Age	x				
Diameter at breast height (dbh)	x				
Crown competition factor (CCF)			x	x	x
Elevation	x				
Habitat Type					x
Latitude	x				
Lodgepole quadratic mean diameter (LPQMD)					x
PGR (Periodic Growth Ratio)		x			
Percent basal area lodgepole pine (%LPBA)			x	x	x

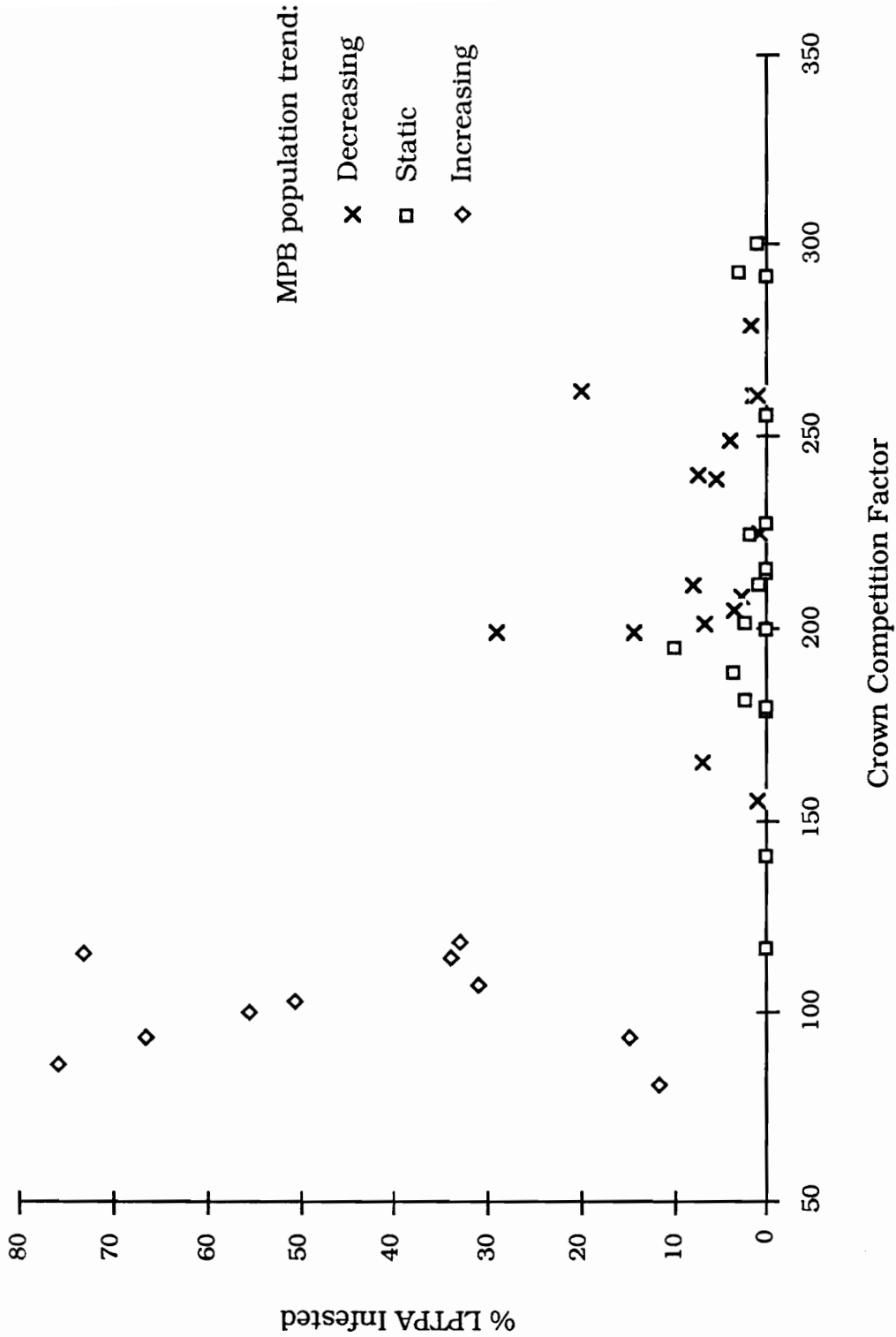


Figure 3.1 Crown competition factor as a function of percent trees per acre lodgepole pine (%LPTPA) infested on the Flathead National Forest. Values are an indication of the MPB population trend at the time of the initial survey (1984).



Figure 3.2. Trees per acre lodgepole pine (TPA) infested by the mountain pine beetle in 3 forests in northern Montana. Current trees per acre infested the year of the survey (1984), the previous year (1983), and 3 years prior (Older) are combined to provide a 5 year cumulative total (Total).

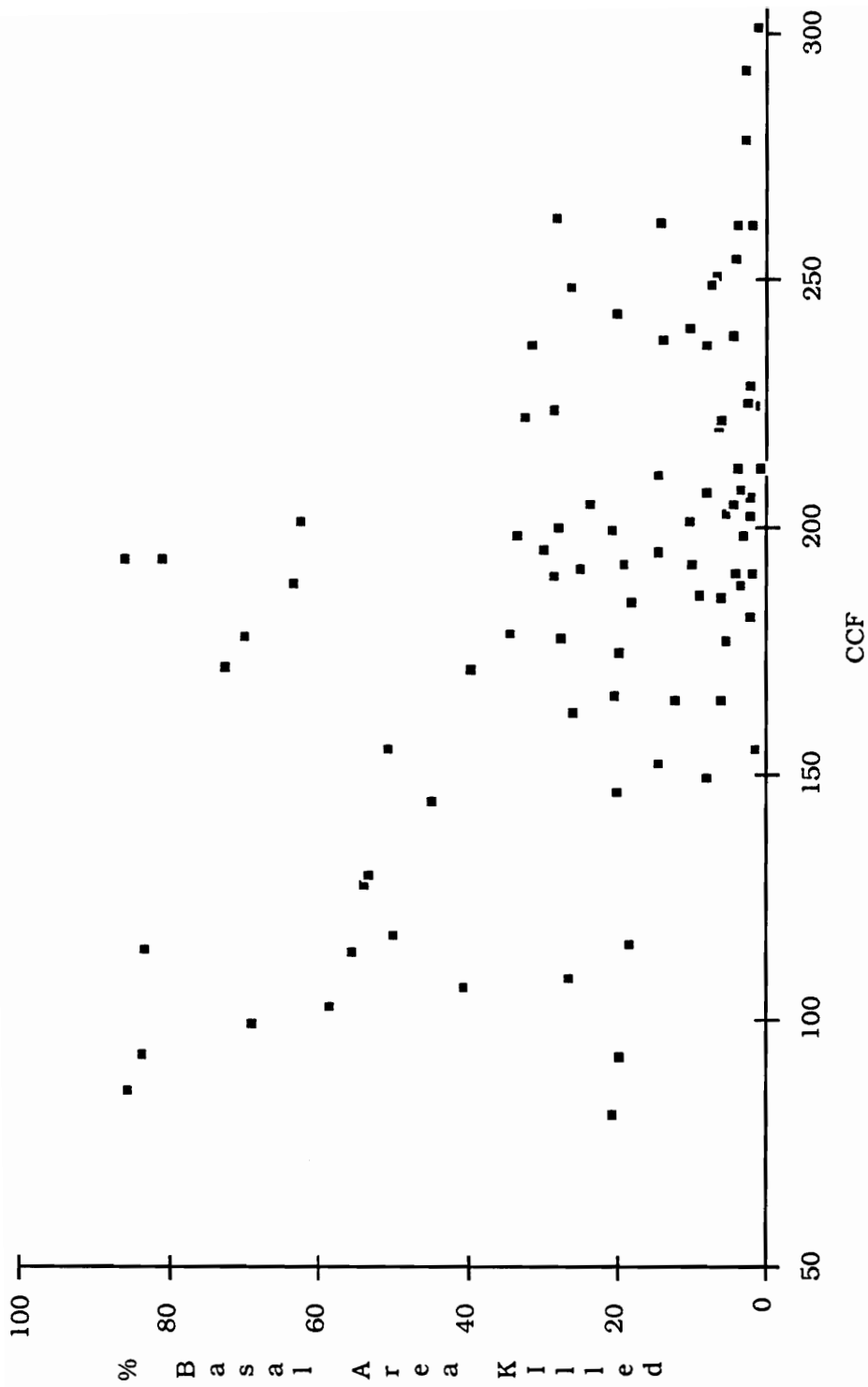


Figure 3.3. Observed percent basal area lodgepole pine killed as a function of crown competition factor (CCF) (Schenk et al. 1980).

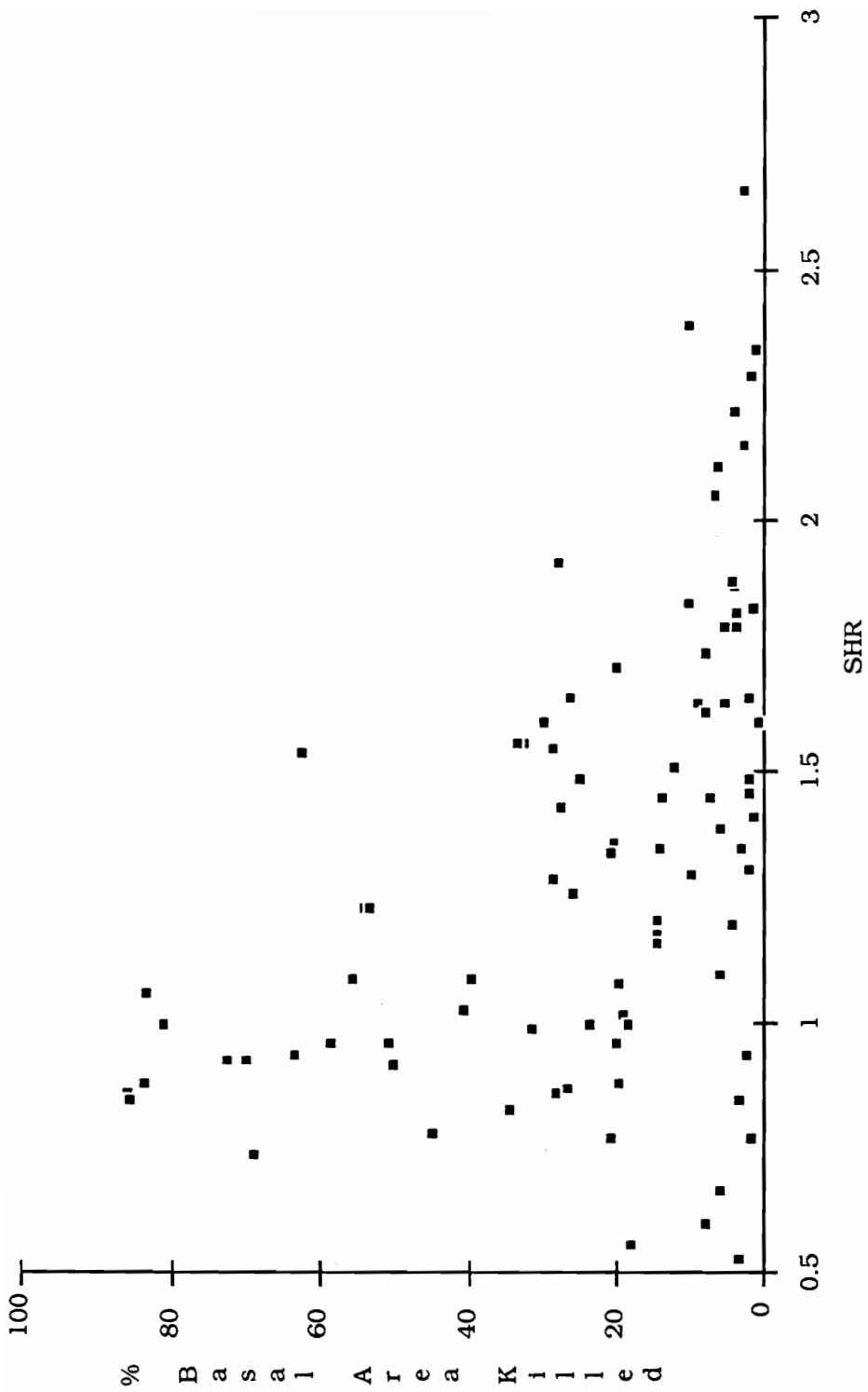


Figure 3.4. Observed percent basal area lodgepole pine killed as a function of Stand Hazard Rating (SHR) (Schenk et al. 1980).

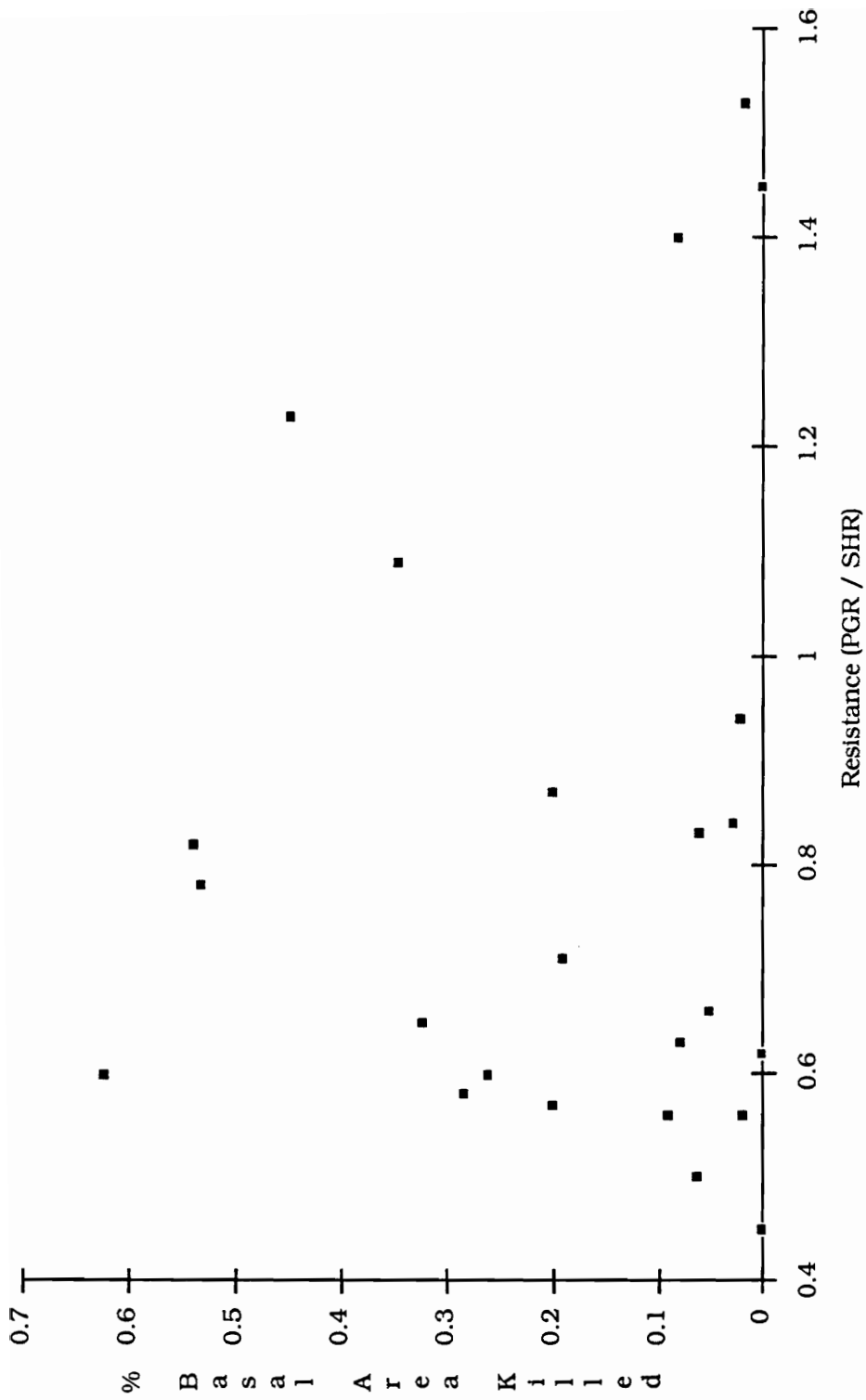


Figure 3.5. Observed percent lodgepole pine basal area killed as a function of stand resistance as defined by Berryman (1978).

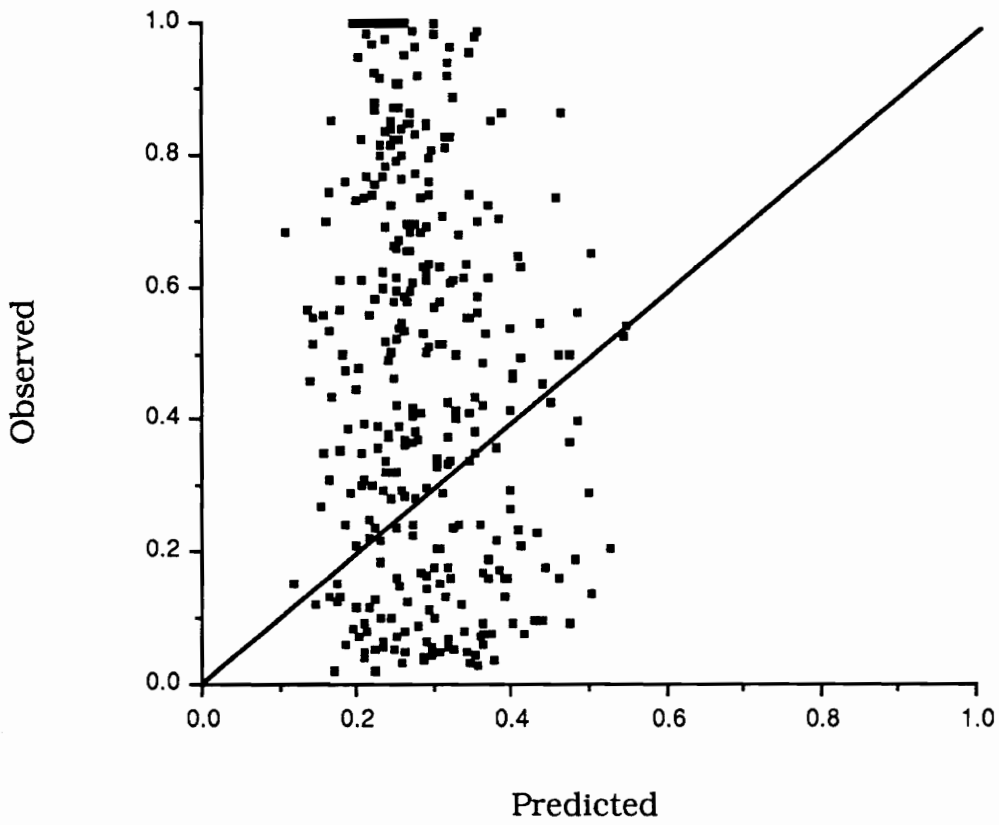


Figure 3.6. Comparison of observed and predicted results from a logistic regression model using density values calculated at the plot level. Values are observed and predicted proportion trees per acre lodgepole pine infested.

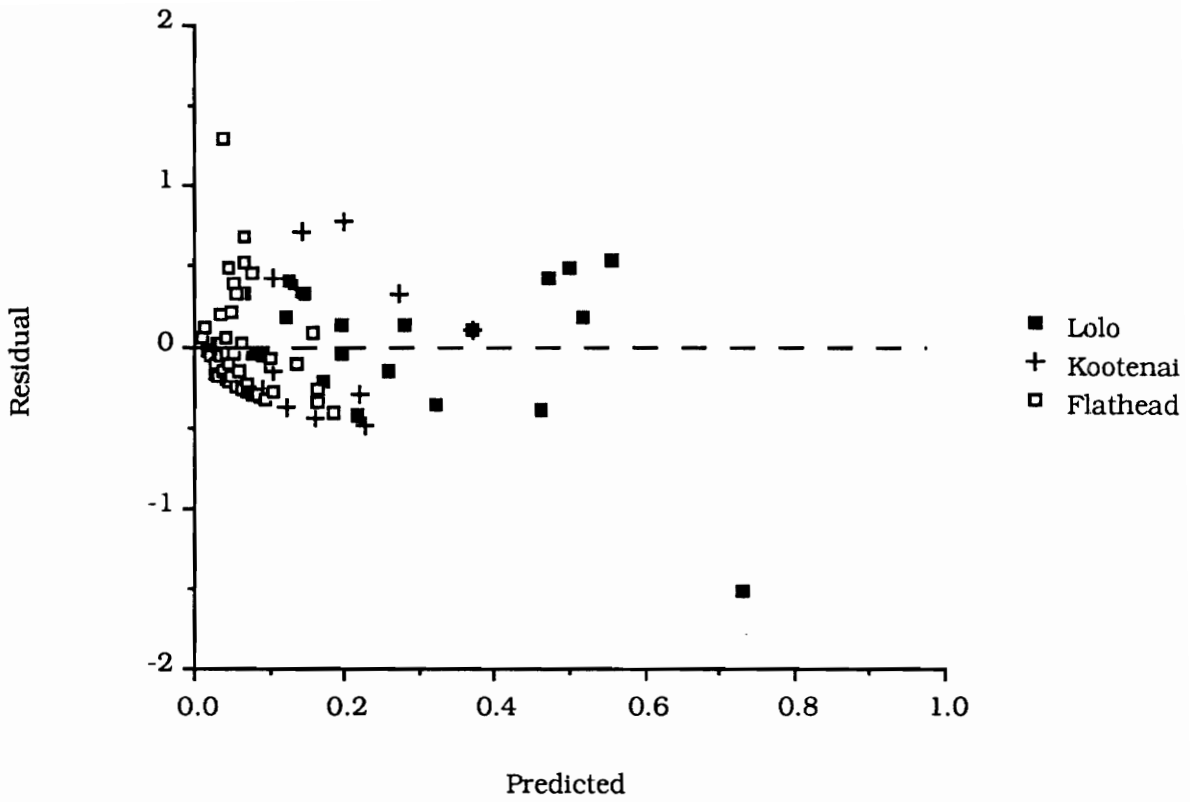


Figure 3.7. Standardized residuals of observed and predicted proportion trees per acre infested in each stand of the Lolo, Kootenai, and Flathead National Forests. Predicted results are from the logistic regression model described in the text.

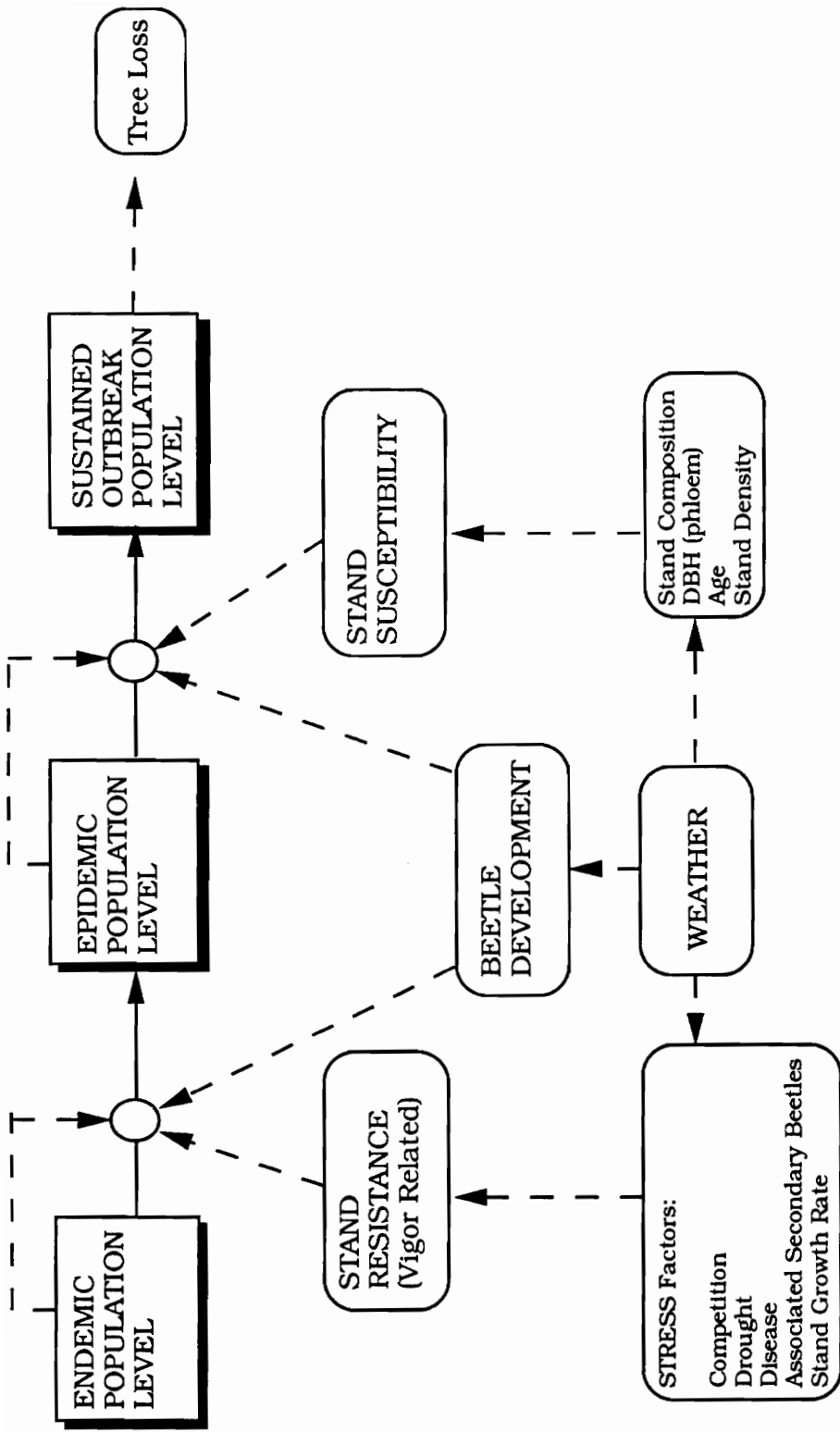


Figure 3.8. Components of the dynamic relationship between MPB populations and LPP stands. Two separate phases are important: 1) the transition from the endemic to epidemic population level, and 2) the growth of an outbreak population, resulting in tree loss. The two phases are dependent, in part, on different stand characteristics. ○ - is the transition probability.

Chapter 4.

A Simulation Model for Predicting Timber Loss in Lodgepole Pine Stands Due to the Mountain Pine Beetle

Introduction

Available data implies that the association between mountain pine beetle (MPB) (*Dendroctonus ponderosae* Hopkins) populations and unmanaged lodgepole pine (LPP) (*Pinus contorta*) stands is governed by a variety of complex interactions and causal factors. Although there are differing opinions on how the factors interact, it is generally accepted that host tree size, stand density, climate, and beetle population pressure have a strong influence on the number and types of trees that will be infested (Cole, W.E. and Amman 1969, Cole, W.E. and Amman 1980, Raffa and Berryman 1980, Safranyik 1978). Efforts to model the MPB/LPP relationship have been diverse.

One group of models were developed to provide a general understanding of the interactions between beetle populations and their hosts. Included in this group is a theoretical model developed by Berryman (1976) which describes MPB emergence density as a function of attack density and habitat suitability. Raffa and Berryman (1986) developed a mechanistic simulation model which includes hypothetically based tree resistance factors and attempts to model both endemic and epidemic population behavior. A model developed by Geizler et al. (1980), which is based on the "switching" behavior of MPB populations, tests specific hypotheses concerning beetle aggregation. These models are useful for providing a framework for evaluating current knowledge of MPB population dynamics and testing hypotheses related to management of LPP

stands. The ultimate goal for the forest manager, however, is to be able to predict the mortality which will occur in a given LPP stand due to MPB populations.

A variety of models have been developed to model timber mortality in a stand due to the MPB. Using simple assumptions of MPB population aggregation, Burnell (1977) developed a model which predicts host tree mortality by diameter class. Cole, W.E. and McGregor (1983) (referred to as the Cole model in the remainder of the paper) used a binomial chain process taken from epidemiology theory to develop a model which estimates LPP mortality as a function of diameter class and beetle population numbers. The Cole model assumes that larger diameter trees are preferred by the MPB, and removes larger diameter trees from a stand before the smaller ones. However, in an analysis of the spatial patterns of MPB attacks, Mitchell and Preisler 1991 observed that the pattern of selection of large and small trees did not change significantly as beetle pressure in the stand increased with time. The Cole model is currently used by U.S. Forest Service silviculturists on the Flathead National Forest.

In an evaluation of the Cole model using MPB permanent plot data from northern Montana, Gibson¹ showed that yearly predictions underestimated the mortality in 6 stands. Gillespie et al. (1990) showed that the model was "reasonably successful" in predicting the basal area remaining in stands in Oregon after a 6 year MPB outbreak. However, they also observed that the model underestimates mortality in the smaller diameter classes, and overestimates mortality in the larger diameter classes. Bousfield and Oakes (in Cameron et al. 1990) noted that when the number of trees per acre was either low or high, the Cole model failed to accurately predict mortality. Cameron et al. (1990) evaluated the Cole model, the Burnell (1977) model

¹ Entomologist, Forest Pest Management, USDA Forest Service, Missoula, MT (personal communication).

and a re-parameterized version of the Cole model (Bousfield and Oakes, in Cameron 1990). Although they found that the Cole model was, in general, the best of the three tested, they noted a substantial amount of unexplained variation in model residuals.

A closer examination of the mechanisms driving the Cole model revealed some questionable assumptions relating to MPB biology and the methods used in model derivation. The model assumes that the probability of tree infestation (mortality) varies among diameter classes, but that mortality in one class at time $t+1$ is affected only by mortality in the same class at time t . In other words, this model assumes that a beetle which attacks a tree in the 5.0 - 7.0 inch diameter class will only attack trees in that same class the following years. This assumption does not adequately depict MPB behavior. Also, in developing the model the probability of a tree not being infested in each diameter class (q parameters) was determined by averaging data from a six-year study. In the final model however, mortality is predicted on a yearly basis.

Unnecessary variance was added in this process. Additionally, most epidemiological studies which use the binomial chain process have a constant cohort size N (Bailey 1975). In the Cole model, N decreases each time step as the dead trees are removed from the pool of susceptibles.

This study was originally initiated to improve predictions from the Cole model for stands in northern Montana by re-parameterizing the model using data from that area. After analyzing the underlying theory of that model however, it was decided that an alternative method would be more appropriate for modeling the temporal loss of trees in a LPP stand due to the MPB. The ultimate goal of the research was to provide silviculturists in north-western Montana with a predictive tool which more closely simulates the influence of MPB populations in a particular stand. With the

information provided by this type of model, LPP stands may be prioritized for silvicultural treatment based on the expected timber loss due to the MPB.

Methods

Data Description

Long term data sets which are ideal for estimating the temporal loss incurred in a stand due to the MPB are not widely available. Data used in this study was from permanent plots established in 1979 by Region 1 Forest Pest Management (FPM) personnel (Gibson et al. 1980). The permanent plot data set contained 10 years of information from each of 30 variable-radius (10 BAF) plots in 4 stands on the Kootenai, Lolo, and Flathead National Forests (Table 4.1). Plots which were harvested during the 10 year study were removed from the data set, resulting in fewer than 30 plots in some stands. Included in the sample for each plot were live trees ≥ 5.0 inches dbh, and an MPB infestation classification for the sampled host trees. Each MPB host tree was classified as: live, currently infested, strip attacked, attacked the previous year, or attacked more than 2 years ago (but not more than 5). Each plot was revisited every year for 10 consecutive years, or until the stand was logged. The full data set contains 1652 trees in the 4 stands. Initial conditions in the stands were similar, although Stand 3 was less dense as represented by the fewer number of trees per acre (Table 4.1). The growth of the MPB population in each stand is represented by the total trees per acre infested for the 10 year period (Figs. 4.1, 4.2, 4.3, and 4.4; note the difference in scale between figures). Stands 1, 3, and 4 were not heavily infested until after the

6th year. Stand 4 was never heavily infested (Fig. 4.4), although conditions for infestation "seemed ideal"².

A C program was written to compute yearly stand densities and mortality in each plot. All stand density measures were calculated on a plot basis in an attempt to describe microclimate conditions important to MPB populations (Bartos and Amman 1989). When a tree became infested by MPB or secondary beetles, it was assumed to die within the year, and was removed from the pool of susceptibles and density calculations for the next year. Output from this program was a data set containing individual tree records and associated plot density measures for each year the tree was alive. Also included in each data record was a measure of the MPB population in the stand, as represented by the number of trees infested the 3 previous years (Lag1, Lag2, Lag3). MPB Lag variables were calculated on a stand basis rather than a plot basis because beetles from one plot will most likely migrate to other plots in the stand.

A subset of this data, consisting of every other plot in each stand, was selected for parameter estimation, and the remaining plots were used for validation (Tables 4.2 and 4.3). Each record in these data sets represented a single tree for each year it was uninfested, and the year it became infested. Therefore each tree could possibly be represented as many as 10 times (assuming it never became infested).

A Probability Model for Host Tree Infestation

A binary response variable was used to describe the infestation probability of a tree. In the data set, an infested tree was classified as a 1 and an uninfested tree a 0.

²Ken Gibson, Entomologist, Forest Pest Management, USDA Forest Service, Missoula, MT (personal communication).

The conditional probability of a tree being infested each year was modeled using the cumulative logistic probability function:

$$P_{1|i} = F(\alpha + \beta X_i) = \frac{e^{\alpha + \beta X_i}}{1 + e^{\alpha + \beta X_i}}$$

where:

$$\beta X_i = X_{i1} * \beta_1 + X_{i2} * \beta_2 + \dots + X_{ip} * \beta_p$$

$\beta = \{\beta_1, \dots, \beta_p\}$ is a vector of regression parameters for p independent variables

$X_{i1}, X_{i2}, \dots, X_{ip}$ is a vector of independent variables for the ith observation

$P_{1|i}$ is the probability of the ith tree being infested ($Y_i=1$)

Because P varies between 0 and 1.0 as $\alpha + \beta X_i$ increases from $-\infty$ to $+\infty$, the logistic function is often used to model the probability of death as a function of other independent variables (Hamilton 1986, Kleinbaum et al. 1982).

When using a binary response variable, the error variance in the regression model is not constant, but depends on the values of the explanatory variables, X_i , resulting in heteroscedasticity (Zar 1984). This violates one of the main assumptions for using ordinary least squares for estimation of parameters. An alternative solution for estimating parameters is the method of maximum likelihood. In this method, the likelihood of obtaining the particular sample of response categories observed in the data set is the joint probability of occurrence of the observed choices (Wrigley 1985). The likelihood function is represented as the product of the marginal distributions of the response variables. The set of parameter values which maximize the likelihood

function, given the available data, are the maximum likelihood estimates (MLE) of the true parameter values. For convenience, the logarithm of the likelihood function is maximized. In this study, the Gauss-Newton method was used to iteratively search for parameter estimates which maximized the likelihood function (SAS Institute 1983). MLE may also be computed using iteratively reweighted least squares, where the weights are the reciprocals of the variances (Strauss and Ikeda 1990 in Preisler 1991).

Statistical tests similar to those used in least squares regression are available for testing hypothesis and goodness-of-fit measures when MLE procedures are used. The MLE chi-square statistic for testing the hypothesis that a parameter is zero is calculated as the square of the parameter estimate divided by its standard error. To test the null hypothesis that all parameters associated with the explanatory variables are equal to 0 (the F-ratio test in least square regressions), the maximized log likelihoods are used and the test statistic is:

$$\text{Log L.R.} = -2[\log\Lambda(I) - \log\Lambda(\beta_{1..p})]$$

where $\log\Lambda(I)$ is the maximized log likelihood of the fitted model which includes only the intercept term, and $\log\Lambda(\beta_{1..p})$ is the maximized log likelihood of the fitted model which includes 1 to p parameters. This test is distributed as chi-square with p-1 degrees of freedom (Wrigley 1985). A likelihood ratio test (ρ^2) is a ratio comparison of maximized likelihood values of the fitted and intercept only model:

$$\rho^2 = \frac{\log\Lambda(\beta)}{\log\Lambda(I)}$$

ρ^2 is the proportion of log likelihood explained by the model and is similar to the squared multiple correlation coefficient r^2 . Instead of an F distribution however, the likelihood ratio statistic has an approximate chi-square distribution under the null hypothesis that parameter estimates equal 0. Although values for ρ^2 range between 0 and 1, its values tend to be considerably lower than the r^2 index. Values of ρ^2 between 0.2 and 0.4 represent a very good model fit (Wrigley 1985). Partial ρ provide a measure of the contribution of explanatory variables independent of the sample size. ρ is zero if the variable provides no partial contribution to the model, and ± 1 if the variable is perfectly related to the response variable. The index C, which is bounded by [-1, 1], is a measure of the rank correlation between predicted probabilities and observed outcomes (Sas Institute 1983).

Several explanatory variables were tested for their ability to describe the variation in the infestation probability for a host tree: stand basal area, lodgepole pine basal area, stand trees per acre, LPP trees per acre, stand density index, LPP stand density index, diameter at breast height (dbh), individual basal area of the tree, stand quadratic mean diameter, average dbh, LPP quadratic mean diameter, habitat, elevation, latitude, number of infested trees the previous year (Lag1), and 2 and 3 years previous (Lag2, Lag3), year of infestation, and a stand indicator variable (ID1, ID2, ID3). The number of infested trees in a stand was used as an indirect measure of the MPB population size. In the original data set, habitat type was recorded for each stand but not at the plot level. Therefore, the stand indicator variable was assumed to be indicative of the habitat type. The individual basal area of a tree was included to see if a more direct measure of the surface area available to the colonizing beetles was more descriptive than dbh alone. The inclusion of population lag variables and a chronology variable, year of the infestation, reduced the effect of time dependent attributes in the

error term of the regression model. Colinearity among explanatory variables was reduced by eliminating redundant and highly correlated variables.

For parameter estimation the data was analyzed in 2 manners: 1) all stands pooled, and 2) all stands pooled with the data ranked by 2 inch diameter classes. A screening algorithm designed for use when the dependent variable is dichotomous (Hamilton and Wendt 1975) was initially used to identify which of the potential variables would be most useful. Results from this process and an intuitive understanding of the MPB/LPP biological relationship were used to develop a series of alternative models. C and ρ^2 were used to test the adequacy of each model. Residual plots by stand and diameter class are included in Appendix I. When examining these plots it should be realized that because the response variable can only take the value 0 or 1, the residuals will typically have a non-normal distribution and may look different from residual plots from least-squares regression procedures. If the predicted probability ($P_{1|j}$) is high, the residual will be small and positive or large and negative. Conversely if $P_{1|j}$ is low, the residuals will be small and negative or large and positive (Wrigley 1985).

Based on a comparison of goodness of fit statistics (C and ρ^2), LPP trees per acre (LPTPA), MPB population pressure the previous year (LAG1), individual basal area of the tree (INDIVBA), year of infestation and the stand indicator variables (ID1, ID2, ID3) were chosen to model the probability of tree infestation. Included in Table 4.4 are parameter estimates and associated statistics for models developed with pooled data and by diameter class. For the pooled data, YEAR and INDIVBA contributed the most to describing the infestation probability ($\rho = .197$ and $\rho = .134$). The MPB population pressure (LAG1) also has an important effect on the conditional probability of infestation ($\rho = .116$). The significance of the LAG1 variable agrees with findings by

Turchin et al. (1991), who showed using time-series analyses that density-dependent effects may be important factors in bark beetle dynamics. Standardized residual plots by stand and diameter class (Appendix I) revealed a general trend of decreasing variability with year of infestation. There was no observable pattern to the data points in these plots with large residual values.

When analyzed by diameter class, the contribution of a particular explanatory variable was dependent upon the class, with the exception of year of infestation. Year was an important influence in all diameter classes due to MPB outbreak population behavior. Tree colonization increases with time as long as there are an adequate number of large diameter trees in the stand (Cole, W.E. and Amman 1980, Mitchell and Preisler 1991). The inverse relationship between individual basal area and infestation probability in the two largest classes is contrary to what would be expected. Research suggests that larger trees are more preferable to MPB populations (Cole and Amman 1969). One explanation is that the infestation was not complete in the stands.

Simulating Temporal Tree Infestation

A quantitative model may be defined as a set of mathematical relationships which are used to gain an understanding of how a system in the real world behaves. A simulation evaluates the mathematical model over a certain time period, gathering data in the process in an attempt to estimate and describe the system (Law and Kelton 1982). To develop a simulation model, simplifying assumptions pertaining to the behavior of the system being studied must first be made. Several assumptions are made for the simulation model described herein which predicts the probability of infestation for each tree in a stand through time:

- Once a tree becomes infested, it dies within the year.

- The beetle population is measured in terms of the number of trees infested in a stand, rather than individual beetles.
- The system being modeled is closed. Therefore, beetle immigration from surrounding stands is not included.
- Growth of a tree within the time period being modeled is insignificant.
- Mortality due to causes other than the MPB is not included.

The previously described probability model, which predicts individual tree infestation by diameter class by year, was used to simulate the course of an MPB infestation in a stand. Based on this function, the probability of a newly infested tree at time t depends, in part, on the infested and susceptible trees at time $t-1$. The probability that an individual tree will become infested is a function of the number of live, susceptible LPP trees (LPTPA) in the plot that year, the individual basal area of the tree (INDIVBA), the number of infested trees the previous year (LAG1) (MPB population size), the year of the infestation, and the habitat type (as represented by the stand number) (see Table 4.3 for parameter estimates). Each diameter class is modeled using parameter estimates specific to that class. Given values for each variable each year, an infestation probability is estimated. This probability is compared to a randomly generated number from the uniform distribution (between 0.0 and 1.0). If the predicted probability of tree infestation is less than the random number, the tree is considered infested and removed from the population of susceptible trees. Otherwise, the tree is considered alive and remains susceptible to the MPB the next year. Infested trees are removed from the density calculations for the following years and included in the LAG1 (MPB population) variable. In this manner, the temporal progression of an MPB population through a stand of trees is simulated, and trees are hypothetically infested based on their susceptibility (as described by the chosen explanatory variables).

Because the developed simulation model has a stochastic component, output from each run will be different even though initial conditions remain the same. The solution from Monte Carlo simulations of this type is the average of many runs of the simulation model. One hopes that as the number of times the model is run increases, the change in the average will become infinitesimally smaller. To determine the appropriate number of runs, a graph was developed depicting the change in the average predicted value from the model as a function of the number of runs of the model (Fig. 4.5). After 50 runs of the model (for Stand 1 data), the average predicted number of trees infested changes less than 1/4 of a tree. This was felt to be an acceptable error, and was chosen as the run size.

Input to the simulation model is in the form of stand data sampled using variable radius plots. This data represents the initial conditions in the stand before an MPB outbreak. Also required is the number of infested trees in the stand the previous year (either real or hypothetical). Because the data the model is based on extends over a 10 year period, the model should only be used for predicting trees per acre infested within that range.

Model Validation

As described previously, a subset of the original data was selected to be used for validating results from the simulation model (referred to as the logistic model in the remainder of the paper). The logistic model was initiated with the first year of data from each plot. These were assumed to be the initial conditions in the stand before the onset of an outbreak. The initial number of trees infested, also required input, was the number observed infested in the stand the previous year (represented by the Lag1 value for the first year). Based on these initial conditions, mortality in each stand due to the

MPB was then simulated for 10 years. This was repeated 50 times, and the average taken.

Because the logistic model was developed in an attempt to improve on predictions from the Cole model, predicted output is compared to both observed values and output from the Cole model. The Cole model was initiated with the same stand conditions as the logistic model and mortality was simulated for 10 years.

Results

Neither the logistic model nor the Cole model were able to accurately predict the large yearly fluctuations in trees per acre infested in a stand, particularly for Stands 2 and 3 (Figs. 4.6, 4.7, 4.8, and 4.9). This may in part be due to the fact that immigration of beetles from surrounding stands is not included in either model. Several attempts have been made to model the dispersal of MPB populations (Safranyik et al. 1989, Polymenopoulos and Long 1990). Including dispersal in the simulation model should increase the capability of the model to predict large yearly fluctuations in beetle numbers. The Cole model portrays the typical bell shaped curve thought to be indicative of an outbreak population through time. Although this trend was apparent in the stand data, it was slightly skewed left and not evenly distributed over the 10 years (refer back to Figs. 4.1, 4.2, 4.3, and 4.4). Predictions from the logistic model appeared to follow the skewed trend slightly better.

In previous evaluations, the Cole model consistently overestimated mortality in the larger diameter classes, and underestimated mortality in the smaller classes. On a stand basis, the Cole model underestimated trees per acre infested in the smallest diameter class (5.0-7.0") in every stand, while in stand 4 infestation was overestimated in all classes (Figs. 4.10, 4.11, 4.12, 4.13). There was no consistent pattern in the

other classes. Overall, 77% of the predictions from the logistic model were within 5% of the actual infestation levels (Fig. 4.14), compared to 23% of the predictions from the Cole model (Fig. 4.15). Note the difference in scale between the two figures.

The logistic model consistently underestimated the total trees per acre infested in each stand over the 10 year period (Fig. 4.16). The Cole model estimated less than the logistic model (and therefore less than observed) in stands 2 and 3, and overestimated infestations in stand 1 and 4. Residual stand basal area predicted by the logistic model was closer to the observed than predictions from the Cole model (Fig. 4.17).

Discussion

An inherent characteristic of MPB population dynamics is the potentiality of rapid increases from endemic to epidemic levels. Endemic populations may subsist for many years in a stand before increasing to the epidemic level. Reasons for the transition are still unclear, although many hypothesis have been put forth and are currently being studied (Gara et al. 1984, Raffa and Berryman 1986, Schmitz 1988). Nonetheless, it is apparent that MPB populations exist in two phases, endemic and epidemic, and that the influence of these two population phases on a stand of trees is quite different.

The goal of the empirical model described in this study is to depict the effect of an MPB epidemic population on a stand of trees. The explanatory variables chosen (see Table 4.4) describe individual tree and stand characteristics which have previously been identified as important in the MPB/LPP relationship at the outbreak level. Output from the model is therefore a prediction of the infestation probability of a tree based on these characteristics. Hence, the empirical model not only describes the particular

situation represented by the data (as is typical of most empirical models), but inherently includes biological knowledge concerning the MPB/LPP relationship in the parameters estimated.

Results from the logistic model were, in general, more accurate than predicted results from the Cole model. Because the logistic model was better at simulating infestation by diameter class, it has more value to managers attempting to predict residual stand structure and diameter distribution. Additionally, the logistic model developed is more indicative of the processes which occur in the MPB/LPP system, compared to the assumptions underlying the Cole model.

Modifications to the logistic model which should be explored include using trees per acre infested for the Lag variables rather than number of trees. Standardized residual plots revealed a decreasing trend in model residuals due to the two time-dependent variables in the model, Year and Lag1 (Appendix I). These variables may need to be transformed. In retrospect, it might be better to not include year at all, due to the fact that it is not always possible to detect when an MPB outbreak will begin in a specific stand of trees. A sensitivity analysis should be performed to identify the key variables and processes that are influencing the dynamics of the system. Also, appropriate techniques for initiating the model when the initial number of infested trees is unknown needs to be explored.

Validation of the simulation model in more than the 4 stands included in this study is necessary to test its adequacy. Backdating stands using growth models is inappropriate and adds additional variance to a system that already has considerably more variance than we can explain. There is a need for more long term (even longer than 10 years) data sets to continue model development and validation of the influence of MPB populations in LPP stands. With long term data sets, time series or Markov

chain analysis could be used rather than a logistic regression. An alternative evaluation of the performance of the simulation model would be to test its impact on stand management decisions made using the output. This could be done in a sensitivity analysis of the advisory system described in chapter 5 which currently uses answers derived from the Cole model.

Table 4.1. Initial stand characteristics (year 1 of the study) based on 10 year permanent plot data from northern Montana. Plots which were harvested during the study are not included. TPA = trees per acre, BA = stand basal area (sq.ft./acre), LPTPA = lodgepole pine trees per acre, LPBA = lodgepole pine basal area, and QMD = quadratic mean diameter (inches).

	TPA	BA	LPTPA	LPBA	QMD
Stand 1 -- Rexford Ranger District, Kootenai National Forest Habitat Type: Abla/Mefe					
N = 444 trees 29 plots	341.8	120.7	269.5	85.5	7.9
Stand 2 -- Plains Ranger District, Lolo National Forest Habitat Type: Abla/Libo					
N = 358 trees 25 Plots	361.0	108.8	297.3	85.6	6.9
Stand 3 -- Tally Lake Ranger District, Flathead National Forest Habitat Type: Abla/Clun					
N = 400 trees 27 plots	201.3	97.4	156.9	67.4	8.8
Stand 4 -- Spotted Bear Ranger District, Flathead National Forest Habitat Type: Psme/Vagl					
N = 450 trees 30 plots	281.9	115.0	221.7	90.3	8.9

Table 4.2. Descriptive statistics for data used to estimate logistic model parameters. This data is a subset of the data described in Table 1 and is denoted by (E). Values are based on plot-level densities. N is the total number of observations in the data set, which may include up to 10 years for any given tree. See Table 1 for stand location and habitat type. TPA = trees per acre, LPTPA = lodgepole trees per acre, BA = stand basal area (sq.ft./acre), LPBA = lodgepole pine basal area, DBH = diameter at breast height (inches).

	Mean	Standard Dev.	Std. Error Of Mean
Stand 1 (E)			
TPA	418.82	133.49	3.88
LPTPA	338.85	134.77	3.92
BA	137.57	38.74	1.13
LPBA	99.21	33.73	.98
DBH	7.91	1.83	.05
N = 1184			
Stand 2 (E)			
TPA	388.78	142.94	4.14
LPTPA	345.28	146.68	4.25
BA	118.02	32.32	.94
LPBA	102.80	36.46	1.06
DBH	7.92	1.62	.05
N = 1192			
Stand 3 (E)			
TPA	246.01	109.93	4.02
LPTPA	166.90	86.28	3.16
BA	119.02	53.84	1.97
LPBA	75.58	29.01	1.06
DBH	10.08	2.29	0.08
N = 746			
Stand 4 (E)			
TPA	334.62	103.49	2.73
LPTPA	305.71	119.09	3.14
BA	119.96	34.14	.89
LPBA	108.47	34.22	.90
DBH	8.73	1.88	.05
N = 1442			

Table 4.3. Descriptive statistics for validation data. This data is a subset of the data described in Table 1 and is denoted by (V). Values are based on plot-level densities. N is the total number of observation in the data set, which may include up to 10 years for any given tree. See Table 1 for stand location and habitat type. TPA = trees per acre, LPTPA = lodgepole trees per acre, BA = stand basal area (sq.ft./acre), LPBA = lodgepole basal area, DBH = diameter at breast height (inches).

	Mean	Standard Dev.	Std. Error of Mean
Stand 1 (V)			
TPA	320.87	133.68	3.47
LPTPA	251.31	131.77	43.42
BA	129.34	49.26	1.28
LPBA	93.04	43.16	1.12
DBH	9.85	4.01	.10
N = 1487			
Stand 2 (V)			
TPA	373.69	128.32	3.90
LPTPA	306.02	143.69	4.37
BA	110.77	28.77	.87
LPBA	84.02	35.54	1.08
DBH	9.58	6.45	.19
N = 1082			
Stand 3 (V)			
TPA	235.22	111.83	3.18
LPTPA	185.11	114.89	3.27
BA	106.99	29.97	.85
LPBA	73.35	32.28	.92
DBH	10.66	3.77	.11
N = 1237			
Stand 4 (V)			
TPA	243.74	67.94	1.67
LPTPA	162.75	85.76	2.10
BA	117.59	26.71	.66
LPBA	81.09	26.27	.64
DBH	10.67	4.27	.10
N = 1660			

Table 4.4. Parameter estimates and goodness of fit statistics for logistic regression model. Parameters were estimated for pooled data and for data ranked by 2 inch (") diameter class. LPTPA = lodgepole pine trees per acre, LAG1 = number of infested trees the previous year, INDIVBA = individual basal area (sq.ft./acre), Year = year of infestation, ID1, ID2, ID3 = stand indicator variables.

Variable	Parameter Estimate	MLE Chi-Square	ρ
Pooled Data			
LPTPA	-.0006	.86	.000
LAG1	.0210	26.48 [*]	.116
INDIVBA	2.16	34.65 [*]	.134
YEAR	.3676	73.07 [*]	.197
ID1	.3682	3.91 [*]	.032
ID2	.6583	8.17 [*]	.058
ID3	-4.44	19.12 [*]	-.097
Intercept	-5.89	182.53 [*]	...
N = 4564 C = .889 $\rho^2 = .27$ Log L.R. = 151.66 (p = .00, 7 d.f.)			
Dbh Class: 5.0" - 7.0"			
LPTPA	-.0047	8.5 [*]	-.162
LAG	.0102	.64	.000
INDIVBA	3.4264	.32	.000
YEAR	.4187	10.39 [*]	.184
ID1	-.2002	.19	.000
ID2	-.9309	1.15	.000
ID3	-8.5886	.12	.000
Intercept	-4.9784	7.91 [*]	...
N = 1110 C = .906 $\rho^2 = .20$ Log L.R. = 63.22 (p = .00, 7 d.f.)			
Dbh Class: 7.1" - 9.0"			
LPTPA	.0007	.46	.000
LAG	.0231	9.28 [*]	.106
INDIVBA	5.30	4.64 [*]	.064
YEAR	.3287	23.44 [*]	.182
ID1	.2680	.99	.000
ID2	.0927	.05	.000
ID3	-9.59	.19	.000
Intercept	-6.98	38.47 [*]	...
N = 1774 C = 871 $\rho^2 = .22$ Log L.R. = 156.05 (p = .00, 7 d.f.)			

Variable	Parameter Estimate	MLE Chi-Square	ρ
Dbh Class: 9.1" - 11.0"			
LPTPA	.0009	.48	.000
LAG	.0268	9.20*	.110
INDIVBA	3.38	2.05	.009
YEAR	.4087	26.87*	.204
ID1	.6182	2.49	.029
ID2	1.44	11.61*	.127
ID3	-3.47	10.66*	-.120
Intercept	-7.17	22.03*	...
N = 1198 C = .899 $\rho^2 = .30$ Log L.R. = 191.63 (p = .00, 7 d.f.)			
Dbh Class: 11.1" - 13.0"			
LPTPA	.0077	6.90*	.156
LAG	.1311	13.13*	.235
INDIVBA	-9.7954	4.82*	-.118
YEAR	.64699	6.87*	.156
ID1	-.1274	.01	.000
ID2	1.3939	1.65	.000
ID3	-10.1318
Intercept	-7.467	.04	...
N = 332 C = .955 $\rho^2 = .51$ Log L.R. = 117.29 (p = .00, 7 d.f.)			
Dbh Class: > 13.0"			
LPTPA	.0042	.29	.000
LAG	.0465	4.4*	.160
INDIVBA	-7.7892	3.49	-.127
Year	.7531	5.67*	.199
ID2	3.4275	4.51*	.164
ID3	-7.254
Intercept	-1.375	.09	...
N = 150 C = .948 $\rho^2 = .38$ Log L.R. = 47.81 (p = .00, 7 d.f.)			

* significant at p < .05

Table 4.4 (cont.)

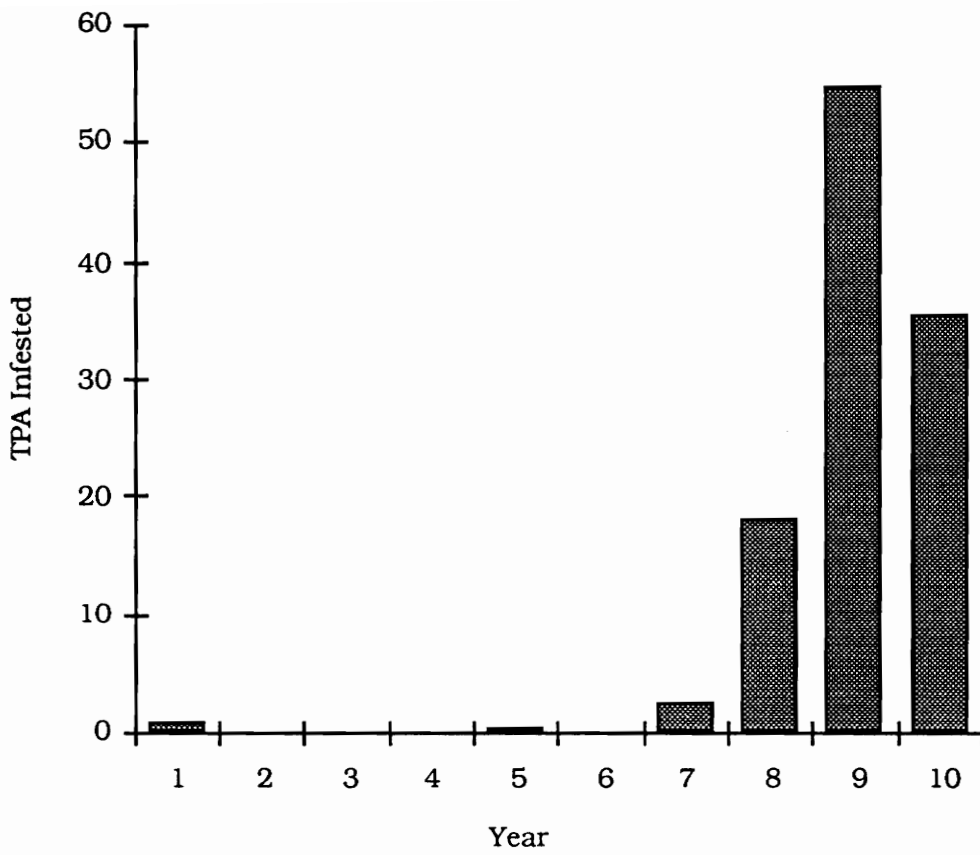


Figure 4.1 Observed trees per acre (TPA) infested in permanent plots in Stand 1 (Kootenai National Forest). See Table 4.1 for stand description.

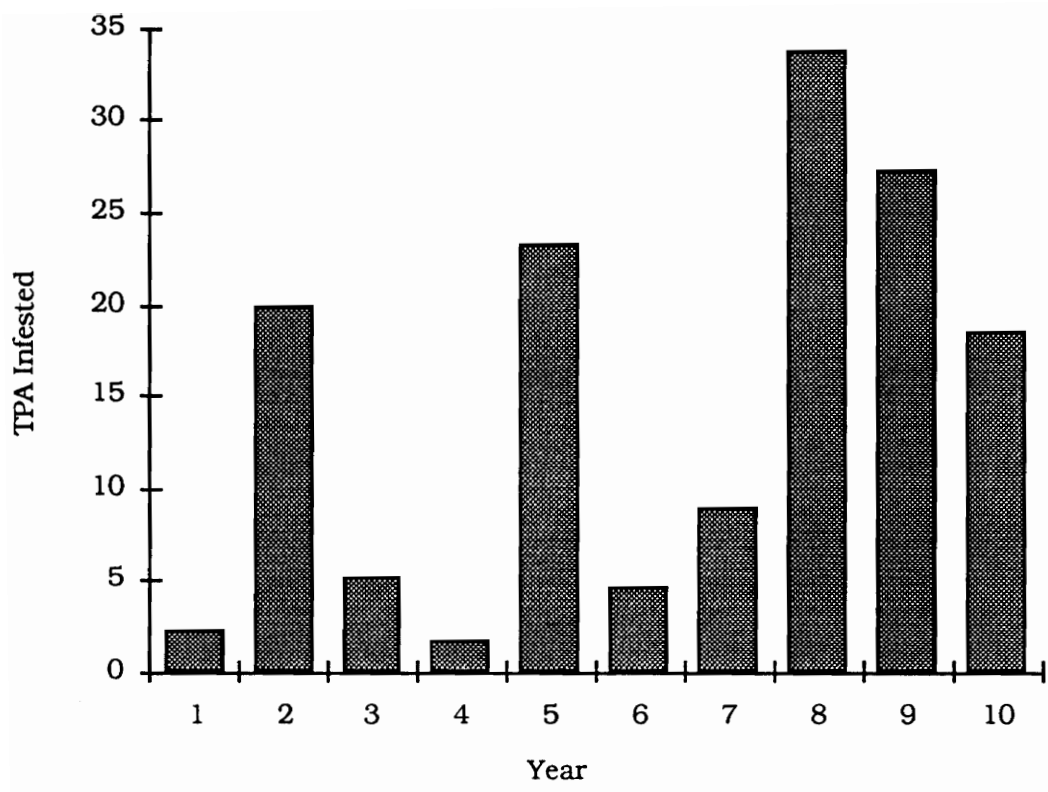


Figure 4.2. Observed trees per acre infested in permanent plots in Stand 2 (Lolo National Forest). See Table 4.1 for stand description.

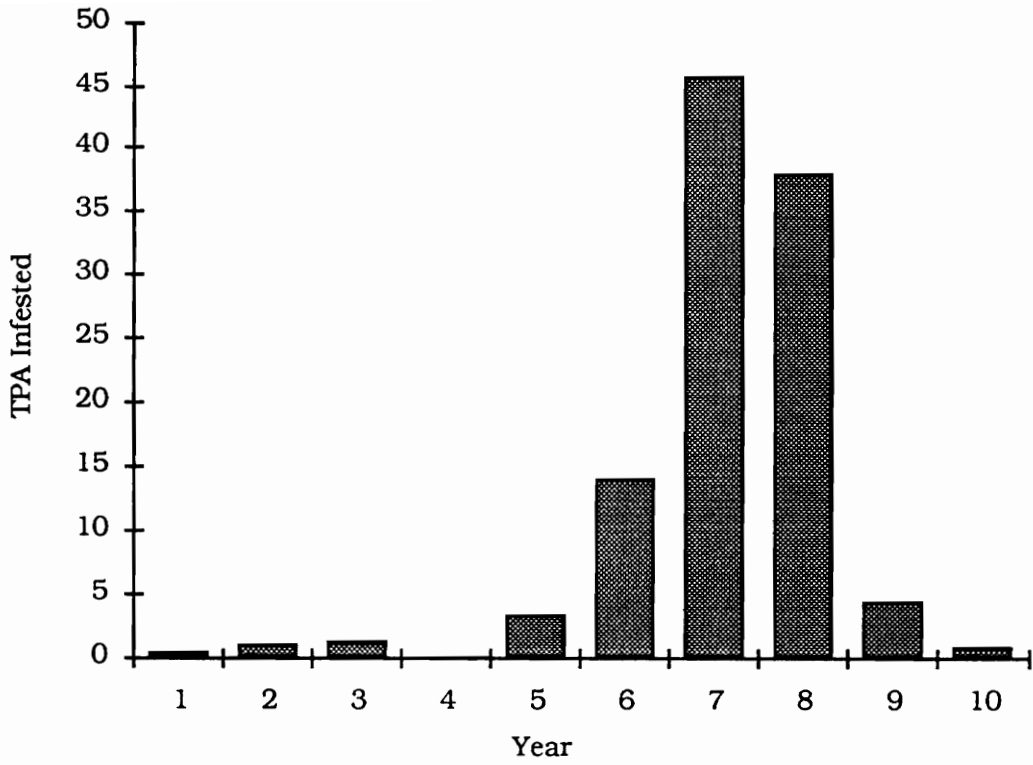


Figure 4.3. Observed trees per acre (TPA) infested in permanent plots Stand 3 (Flathead National Forest). See Table 4.1 for stand description.

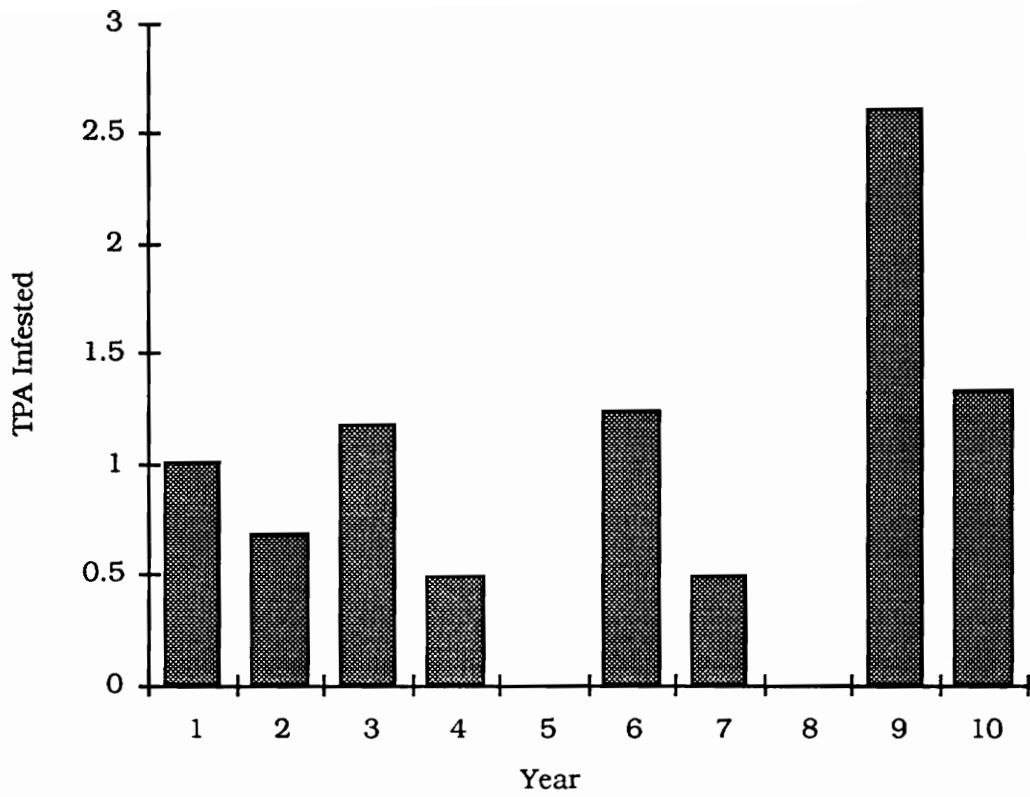


Figure 4.4. Observed trees per acre (TPA) infested in permanent plots in Stand 4 (Flathead National Forest). See Table 4.1 for stand description.

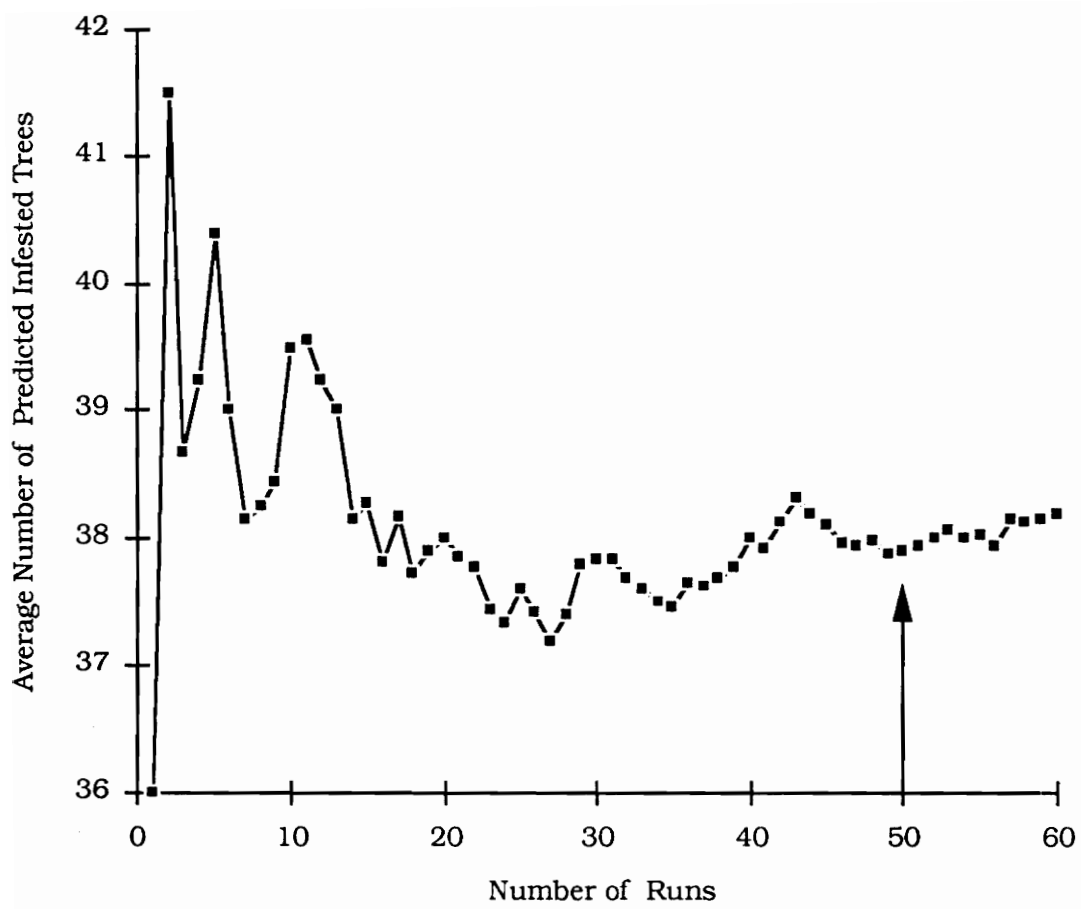


Figure 4.5. Predicted number of trees infested from the simulation model, averaged over the number of runs of the model. Based on this graph, 50 runs of the model was determined to be an acceptable number for predictive purposes. Average trees infested changed less than 1/4 of a tree after that number.

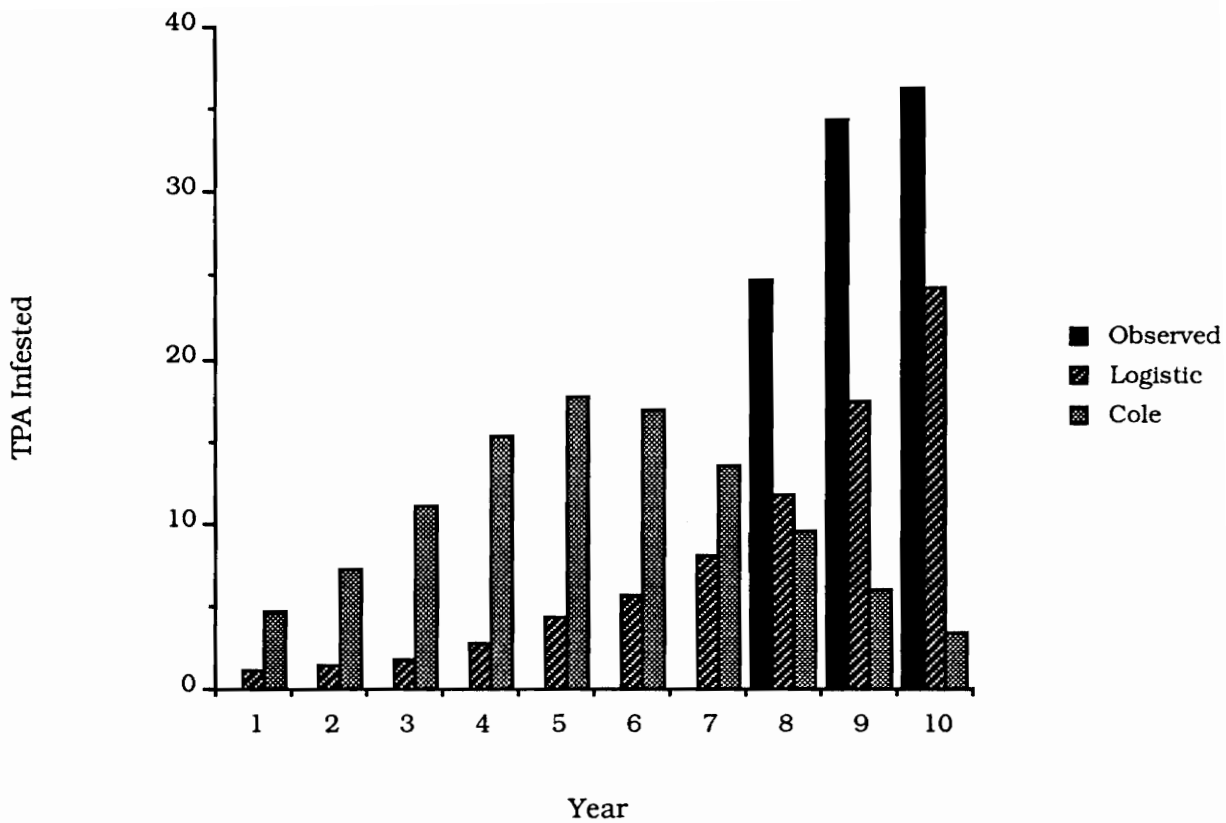


Figure 4.6. Observed and predicted trees per acre (TPA) infested by year for Stand 1. Predicted results are from Logistic and Cole models using data described in Table 4.3.

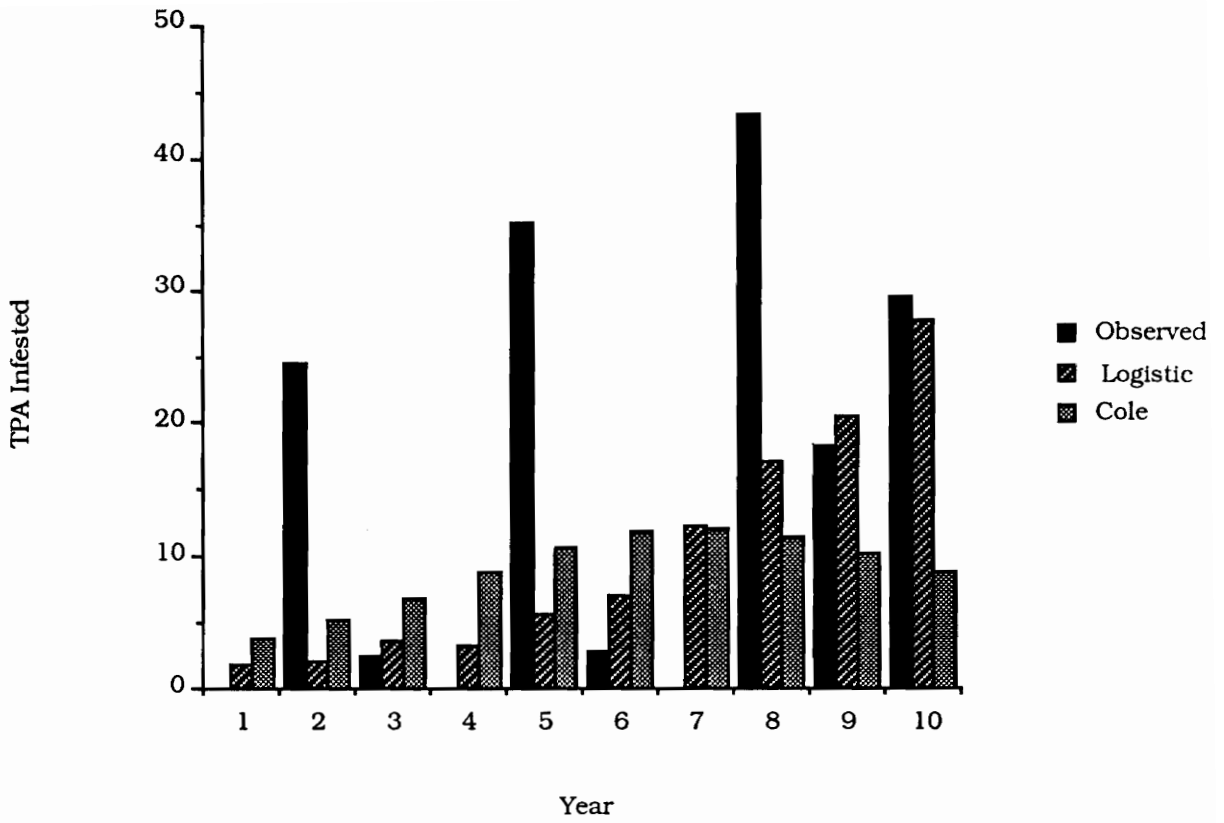


Figure 4.7. Observed and predicted trees per acre (TPA) infested by year for Stand 2. Predicted results are from the Logistic and Cole models using data described in Table 4.3.

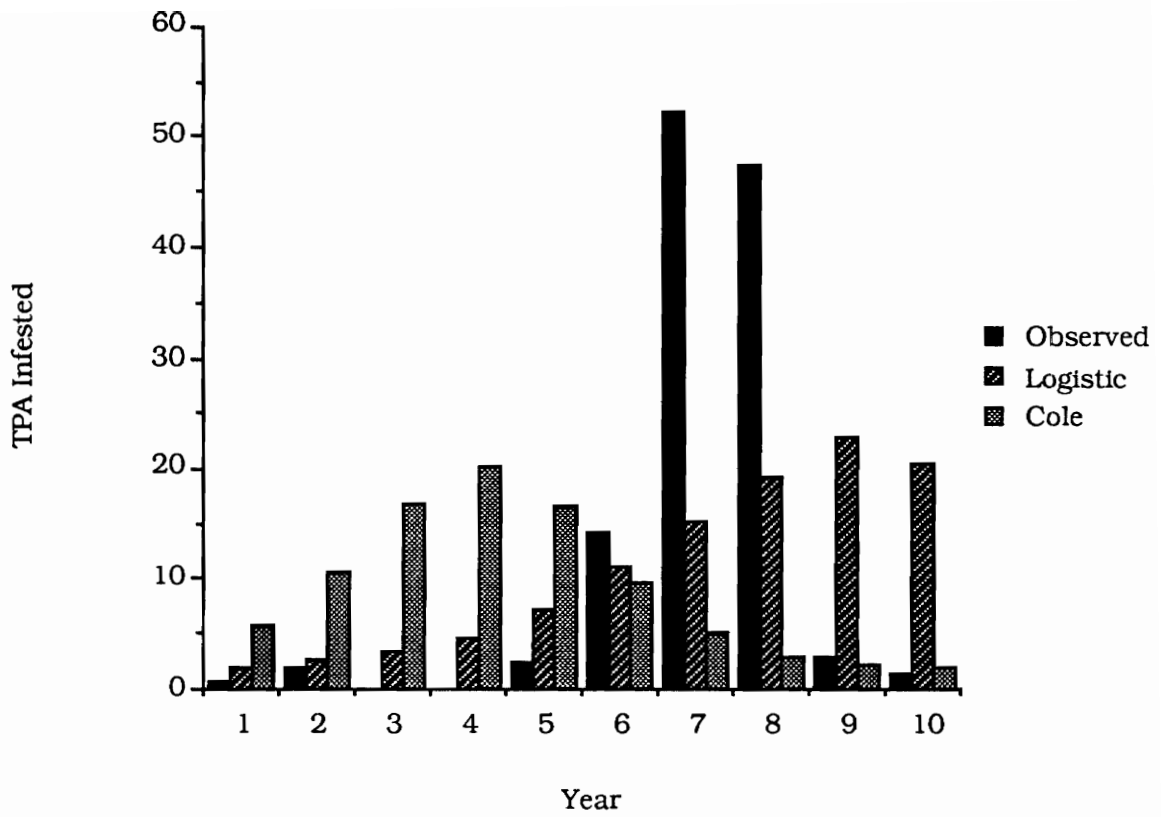


Figure 4.8. Observed and predicted trees per acre (TPA) infested by year for Stand 3. Predicted results are from the Logistic and Cole models using data described in Table 4.3.

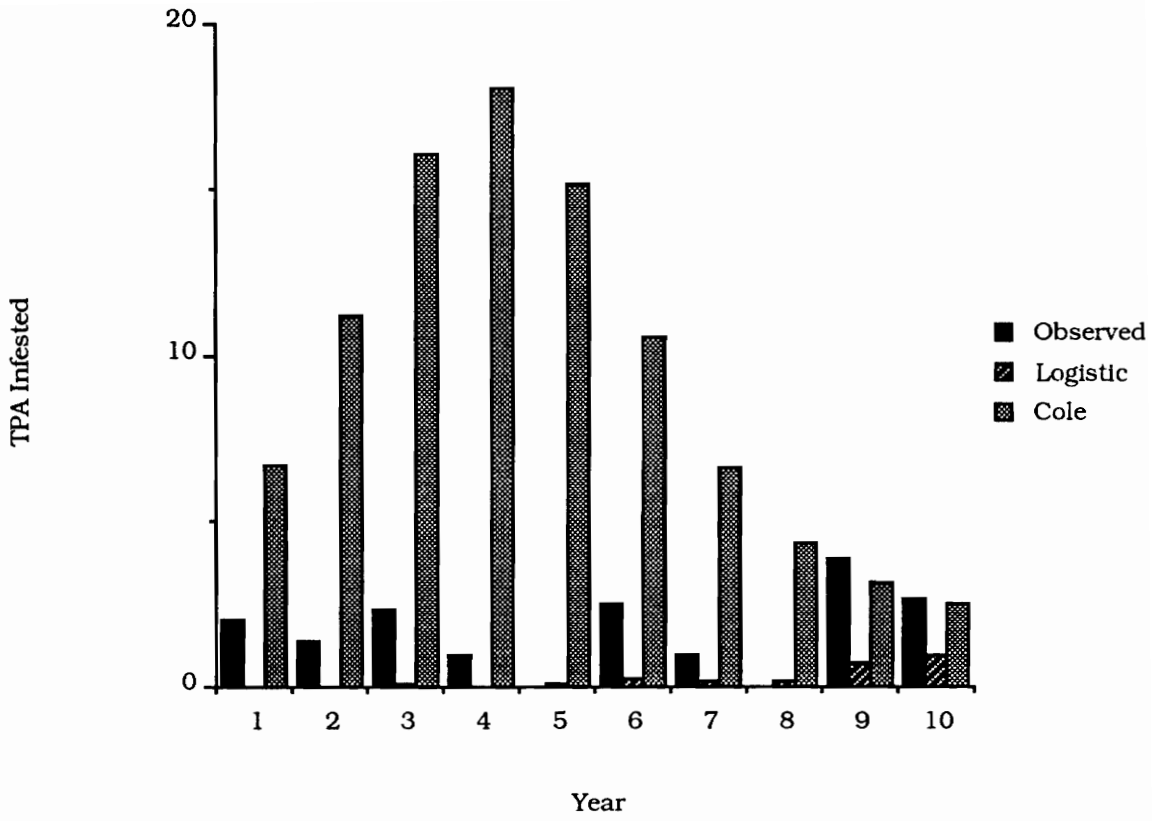


Figure 4.9. Observed and predicted trees per acre (TPA) infested by year for Stand 4. Predicted results are from the Logistic and Cole models using data described in Table 4.3.

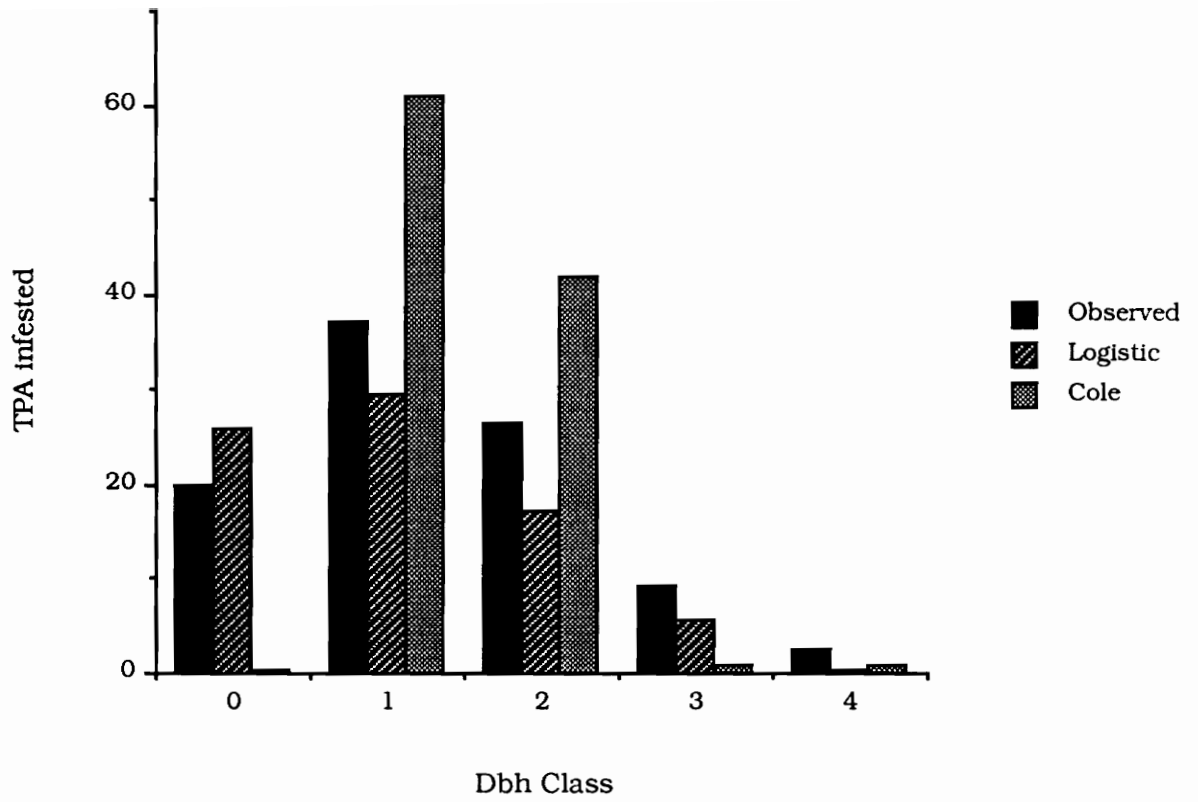


Figure 4.10. Observed and predicted trees per acre (TPA) infested by dbh class for Stand 1, all years combined. Predicted results are from Logistic and Cole models using data described in Table 4.3.

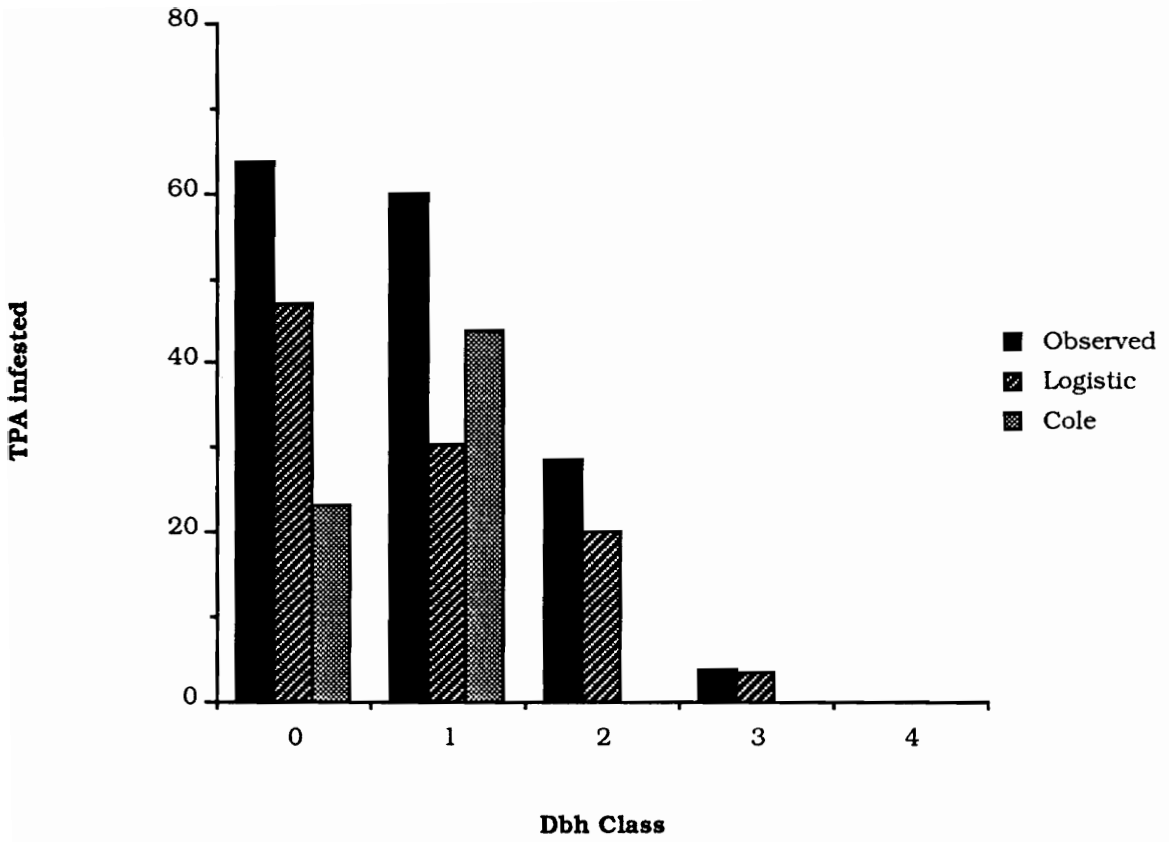


Figure 4.11. Observed and predicted trees per acre infested by dbh class for Stand 2, all years combined. Predicted results are from Logistic and Cole models using data described in Table 4.3.

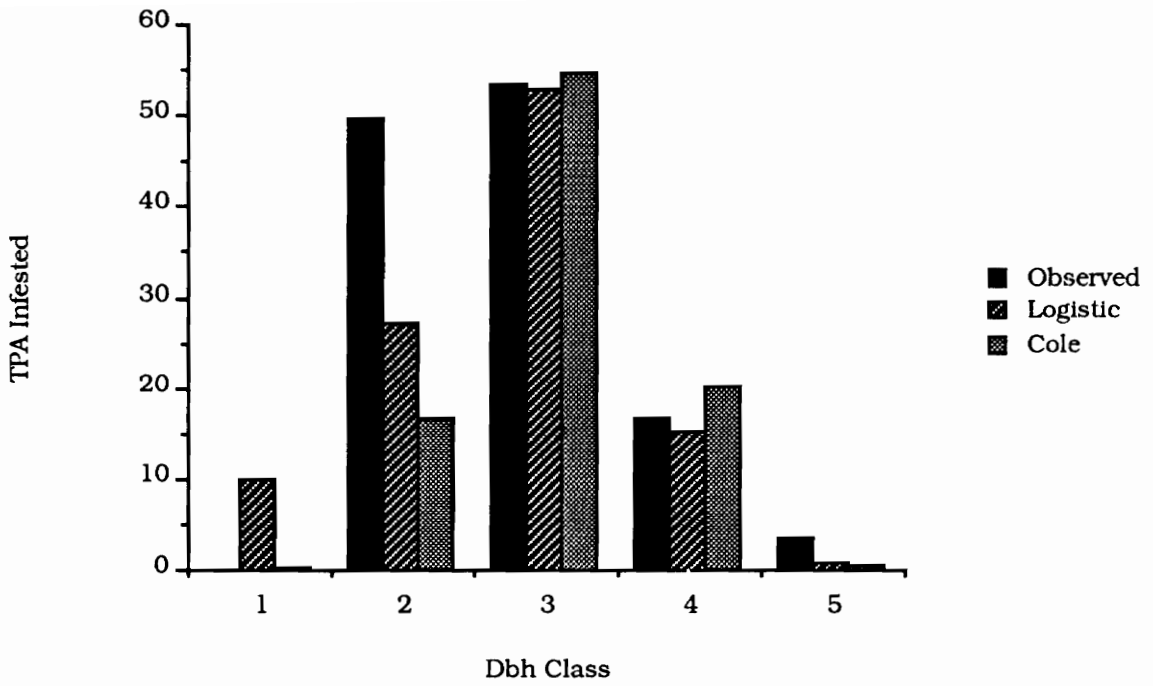


Figure 4.12. Observed and predicted trees per acre (TPA) infested by dbh class for Stand 3, all years combined. Predicted results are from the Logistic and Cole models using data described in Table 4.3.

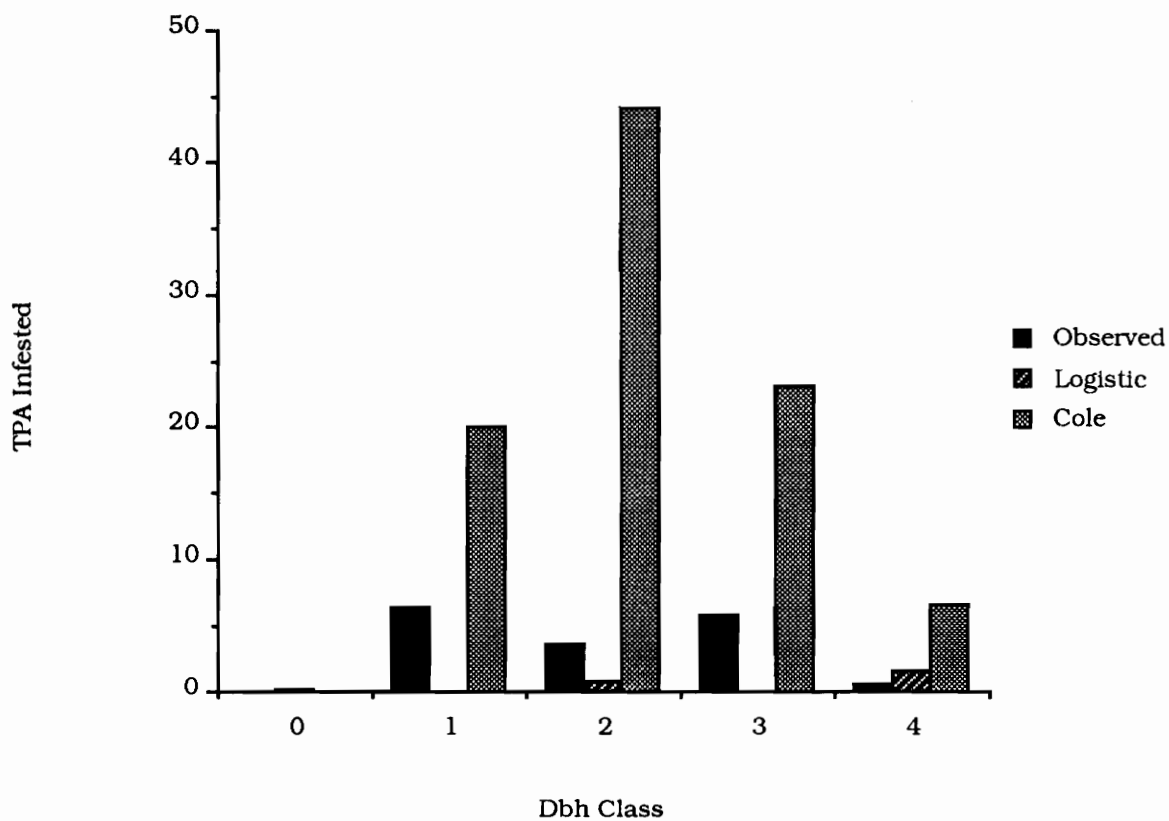


Figure 4.13. Observed and predicted trees per acre (TPA) infested by dbh class for Stand 4, all years combined. Predicted results are from the Logistic and Cole models using data described in Table 4.3.

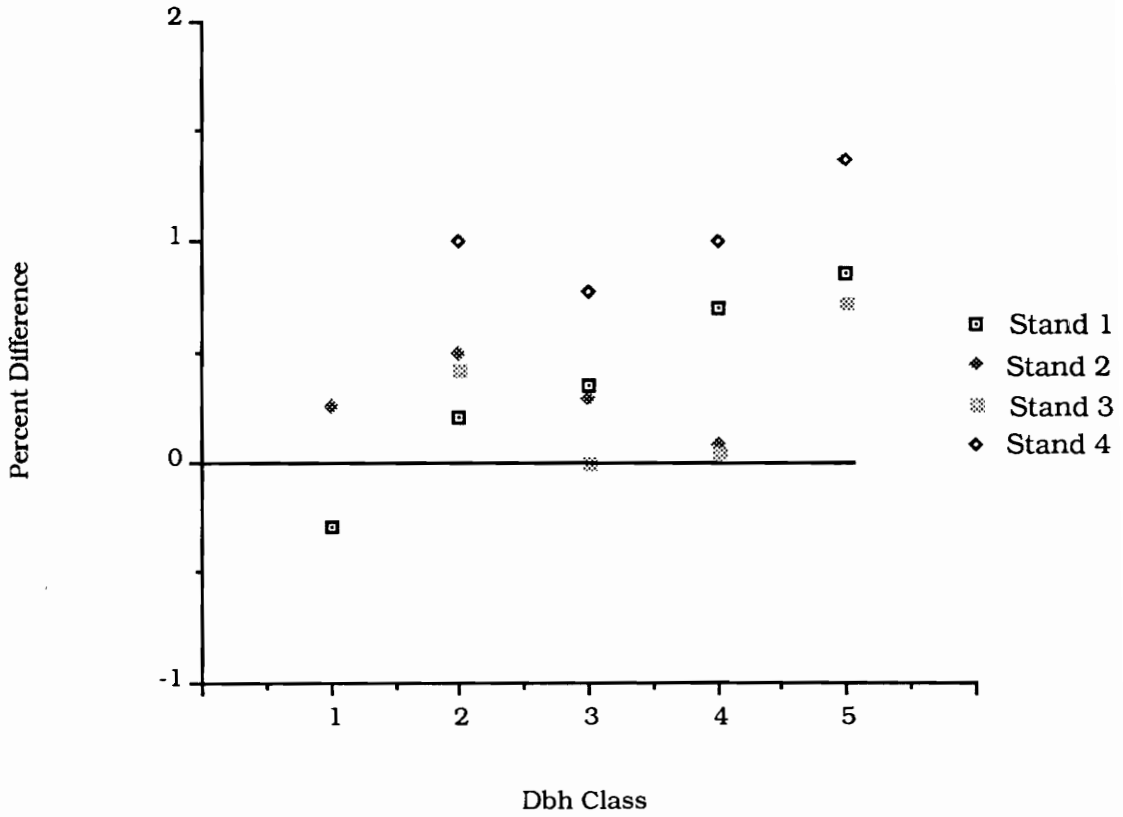


Figure 4.14. Percent difference, $(\text{observed} - \text{predicted})/\text{observed}$, trees per acre infested by Stand and diameter class. Class 1 = 5.0-7.0", class 2 = 7.1-9.0", class 3 = 9.1-11.0", class 4 = 11.1 - 13.0", class 5 = > 13.0". Predicted results are from the logistic model.

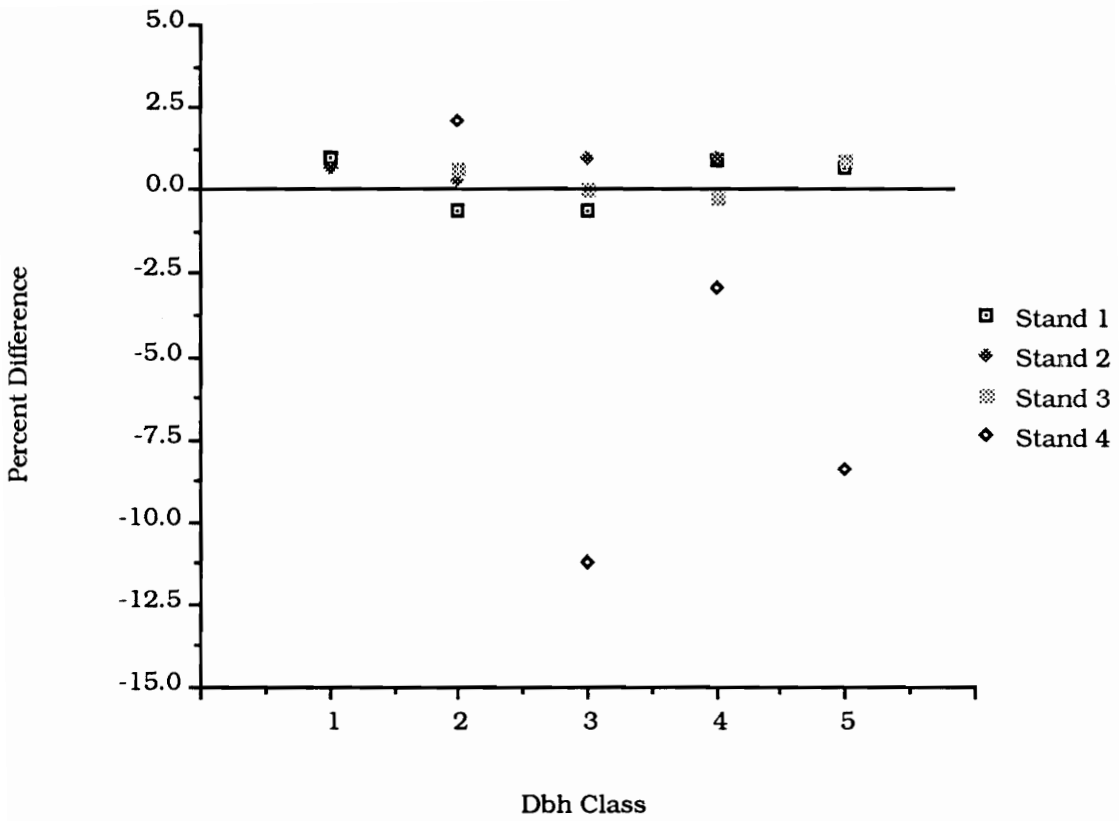


Figure 4.15. Percent difference, (observed-predicted)/observed, trees per acre infested by Stand and dbh class. Class 1 = 5.0-7.1", 2 = 7.1-9.0", 3 = 9.1-11.0", 4 = 11.1-13.0", 5 = >13.0". Predicted results are from the Cole model.

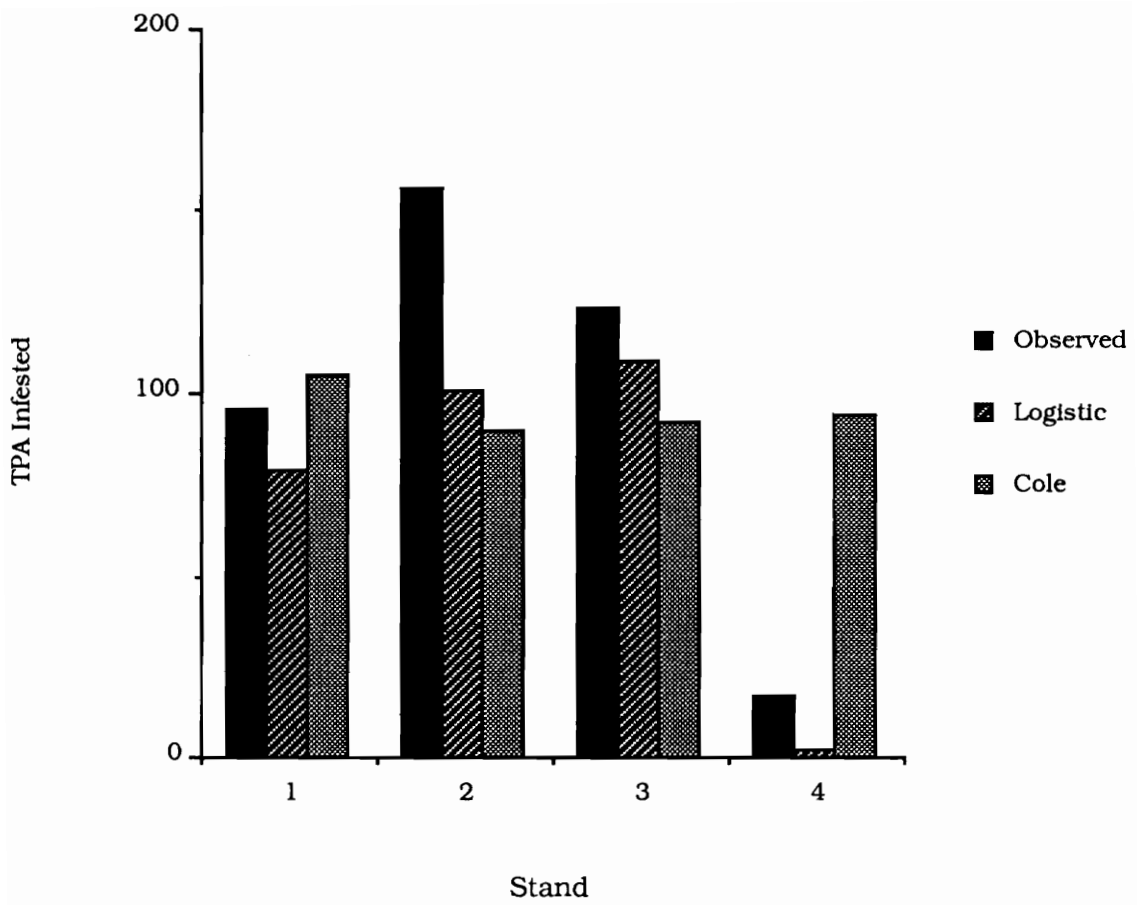


Figure 4.16. Total observed and predicted trees per acre (TPA) infested (by Stand) for 10 years. Model predictions are from the Logistic and Cole models.

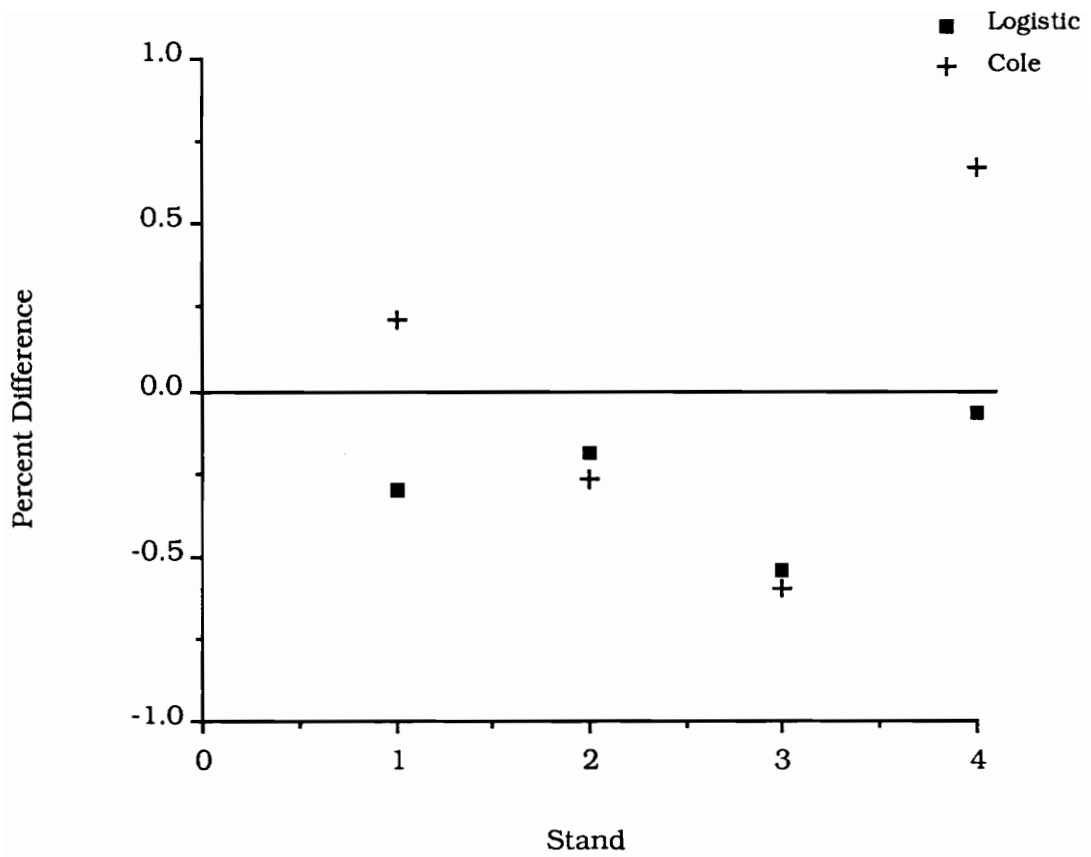


Figure 4.17. Percent difference, $(\text{observed} - \text{predicted})/\text{observed}$, in residual basal area in each Stand after a 10 year MPB outbreak. Predicted results are from the Logistic regression and Cole models.

Chapter 5.

An Advisory System for Mountain Pine Beetle Management in Northern Montana

Introduction

U.S. Forest Service silviculturists must balance multiple resource uses and varied public interest with knowledge of silvics and economics to determine an appropriate silvicultural prescription for all stands on a National Forest. A silvicultural prescription documents the proposed objectives for a stand and the schedule of activities, including dates for each treatment. To reduce widespread losses to the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) (MPB) in lodgepole pine (*Pinus contorta*) (LPP) stands, silviculturists must consider MPB populations when developing their prescriptions. This will require efficient transfer of knowledge about the MPB from research to management in a timely, usable fashion, as well as a means for organizing and synthesizing the information. Knowledge transfer among silviculturists is also desirable so that innovative strategies can be passed to others attempting the same or similar task. Since the early 1960's computers have been successfully used for these purposes (Coulson et al. 1987). One computer technology in particular which can help managers with this task is a knowledge-based system.

Knowledge-based systems are a collection of simple facts and general rules that symbolically represent the knowledge specific to a particular task (Davis 1986). A knowledge-based system is not limited to problems which are numerically tractable, but takes into account qualitative information as well. Expert systems, the most common type of knowledge-based system, contain a knowledge-base which describes the thought processes a human expert uses to solve a problem. They also may

incorporate external routines, often quantitative models, which are not part of the reasoning process but provide required information (Plant and Stone 1991). In this manner, integrated knowledge-based systems act as a framework to bring together the different components needed for making timber management decisions which include strategies for MPB management in lodgepole pine stands.

The first step in building a knowledge-based expert system is to identify the domain of the problem. Therefore, the initial objective of this research was to define the decision model of U.S. Forest Service silviculturists who currently include strategies for MPB populations in their lodgepole pine stand management process. From this a computerized knowledge-based system which synthesizes the required qualitative and quantitative information was developed to aid managers in making these decisions.

Knowledge Acquisition

In response to several widespread outbreaks, silviculturists have recently applied innovative strategies for MPB management on three National Forests in Northern Montana (Beckley 1989, Call 1989, VanDenburg 1989). These forest managers have gained insight into the difficult process of integrating lodgepole pine management with strategies for reducing timber losses due to MPB populations. Additionally, MPB population data exist for these forests. I therefore chose to model the decision process of the U.S. Forest Service personnel managing these forests.

Question probes, a structured interview process for eliciting knowledge (Gordon and Gill 1989) was used to obtain information from silviculturists on these forests, as well as from Forest Service entomologists and research scientists (Table 5.1). In specific terms, knowledge may be defined as information in context (Plant and Stone 1991), and may be separated into two categories (see Table 1.1). Declarative knowledge

describes the objects and their attributes, while procedural knowledge describes relations between the objects and is manifested in their actions. In the question probes technique, the interviewer asks structured questions to map a knowledge network which represents the declarative knowledge.

A knowledge network is a graphical method for representing specific concepts and their relationships (Gordon and Gill 1989). In the initial interview, only the most fundamental and basic concepts which help to identify the scope and intended purposes of the system are acquired. Each concept is represented as a node in the network. As each node is added, it is tagged to identify the source of the information (e.g. from a simulation model, data set, etc.). For each node, a set of questions are then prepared which help to expand the node. In subsequent interviews, these questions are used to verify and complete the network. One section of the network is represented in Figure 5.1. Procedural knowledge that links these nodes together and provides information about how the expert performs the task is indirectly obtained through scenarios and by watching the expert solve a particular problem.

The initial interviews, in which the scope and intended purposes of the system were identified, helped to avoid an "unsuccessful success" (Dyer 1987), a system that does what it is supposed to do, but is never used. Because the silviculturists interviewed are also targeted users, their role in designing the system increases the probability that the final product will be used (Gordon et al. 1987). Additionally, by doing this, required information for the system was, for the most part, isolated to that already available to the manager. In these sessions, it was determined that the scope of the system should be bounded to a subset of the more complex silvicultural prescription process. The primary decision for the resource manager is to decide what, if any, alternative management responses to an imminent MPB outbreak population

should be considered. In essence, the system described herein reflects the process of determining the appropriate silviculture treatment when the MPB is a mediating factor. This system does not include scheduling activities. Additionally, timber is the only management objective considered. An expert system which includes a more comprehensive knowledge base for describing the entire silviculture prescription process is currently being developed in Region 1 of the U.S. Forest Service¹.

Many discrete decisions are required for effective forest pest management, and separate reasoning processes are often used for each. Declarative and procedural knowledge elicited during the interview sessions provided information necessary to solve each independent decision. In this manner, each decision could be modeled separately. One method for evaluating this type of decision process is a function model. Function modelling is a method for building a network of related, discrete decisions which when put together model the entire decision process (Stone 1989). This decision network is analogous to a classical flow model of physical systems, but the state variables are replaced with decisions and the linkages between the nodes represent information flow. The manner in which the decisions are put together model the inherent procedural knowledge.

Figure 5.2 is a function model describing the decision process of silviculturists on the Flathead National Forest for determining a stand treatment when MPB populations are an influencing factor. Five treatment options (Table 5.2) were identified in the interview process, along with the necessary conditions to satisfy each option. Each box represents a separate decision which must be made before the final goal, the appropriate silvicultural treatment for the stand being considered, may be decided

¹Jim Chew, Silviculturist, USDA Forest Service-Region 1, Missoula, MT (personal communication).

upon. A decision may be based on information acquired from either a data set, results from a simulation model, or the results of a previous decision. This information flow is represented by the solid lines. For example, the expected loss in a stand due to the MPB, which depends on stand and beetle information, is required to choose an appropriate silvicultural treatment.

System Development

A prototype system was initially developed on an Apple SE using Supercard². The flexibility of this software provided an easy method for designing the architecture of the system. Using the prototype, the intended flow of information and optional components in the system were presented to potential users, and comments and suggestions obtained. This design was then used for development of the MPB Advisory System on a Compaq386 using Goldworks, an expert system development language, and Common Lisp³. Goldworks provides an inference engine with backward, forward, and integrated (a mixture of backward and forward) chaining, as well as some object-oriented capabilities. Goldworks also has a version for the operating system on the Data General (DG) which is the computer system used by the US Forest Service. Therefore, the developed system can ultimately be transferred to the DG for use at the U.S. Forest Service District Office level.

²Supercard is a Hypercard type language developed by Silicon Beach Software.

³Gold Hill Computers, Inc.

Knowledge representation

Knowledge in the system is stored in two forms: 1) rules, and 2) frames.

Qualitative information acquired during the interviews, which describes the procedures and constraints of the decision-making process, was translated into if-then rules.

Frames were used to hierarchically structure both quantitative and qualitative data. A frame is a data-structure for representing a class of objects or situation (Minsky 1975).

Attached to each frame are several kinds of information representing both declarative and procedural knowledge. Instances represent the specific entities of a frame, and

slots are used to assign attributes to the objects represented by an instance. When the instance of a frame is asserted, values are put in the slots. In the example in

Figure 5.3, the stand identified by 'Flathead_01234' is an instance of the frame

Stand_Information, with slot values age: 80, dbh: 16.4", slope: 18% and BA: 120 ft.².

Hierarchy in the system provides the capability for a frame to inherit all slots from its parent frames and ancestors, and passes on all of its slots to its child frames. Frames can also include functions which act on other frames, and therefore provide object-oriented capabilities. The frame structure for the system is represented in Figure 5.4.

Rules in the knowledge-base were partitioned into rule-sets according to their task. Each rule-set has associated with it an enabling pattern. When a goal-rule has a pattern that matches the enabling pattern, that rule-set is enabled for use. This way, rules are searched only as needed and the knowledge-base can be more easily altered.

In the rules, constraints for each prescription treatment were divided into 2 categories:

1) those contributing to conditions of the residual stand after the treatment has been performed, and 2) those contributing to economic concerns when choosing a particular treatment. Based on the available stand and beetle information, the optimal treatment is the one which would provide the best residual stand and economic benefits. Each

treatment option is ranked as providing good, moderate or poor economic and residual stand conditions (based on information obtained in the interview sessions). This approach mimics the way in which a manager might compare the results of a particular treatment for each stand, choosing the one which provides the best economical and ecological benefits (Fig. 5.5). This method of structuring the knowledge provided categorization of the information needed for each decision, eliminating the need to use numerical rankings such as certainty values.

Stand survey data is currently accessed in the form of the U.S. Forest Service Forest Pest Management Insect and Disease Survey Forms. However, only slight changes would be necessary to input any other type of stand survey information such as R1EDIT data files used on National Forests in Region 1. Several quantitative algorithms are automatically accessed by the system to provide additional information as needed to make a decision. Simple algorithms are coded in Lisp and included as part of the system code. More complex statistical and simulation models are resident in the DOS operating system as executable files (both Fortran and C), and are automatically called by the system as needed. The ability for frames to call functions when slot values are changed is a desirable feature of the Goldworks software. Models currently accessed include INDIDS (Bousfield et al. 1985), and a model for determining the expected timber loss in the stand due to the MPB (Cole, W.E. and McGregor 1983, Chapter 4). INDIDS computes mensurational values from the stand survey data, providing measures including basal area, trees per acre and volume. The rate-of-loss models are used for prioritizing stands for treatment, based on the amount of loss they will sustain. Results from these models are stored as slot values in the appropriate frame. In the future, the system will be able to access additional models for providing information on MPB phenology and risk classification.

System Flow

In addition to a knowledge base, an expert system also contains an inference engine. The inference engine is the part of the system containing elementary problem-solving logic which operates by searching through the knowledge base and applying rules to the current data. In rule-based systems, the inference engine either uses rules to reason forward from observations to conclusions, or backwards, from a goal hypothesis to the data that might refute the hypothesis (Davis 1986). A mixture of both forward and backward chaining is used in this system to determine the appropriate treatment.

Initially the user is queried for the name of an input file which contains stand survey data. This file is automatically run through the INDIDS program. Original stand and site information and additional mensurational output from INDIDS are then written to a file in a Lisp format. This file is read into Goldworks and the data stored as slot values of an instance (with a name equal to the stand identification code, e.g. Flathead_01234) in the Stand_Information frame. Currently, only one stand may be entered into the system at a time. The user is then asked for stand topological information to be used in determining the hazard to tree blow down (Alexander 1986). The user must also input information about the presence of MPB populations in the management unit. Hopefully, in the future this type of information will be included in the stand survey data set initially input to the system, minimizing the amount of user input required.

Goldworks uses special structures called attempts to initiate goal-directed reasoning (backward chaining). An attempt consists of a pattern that corresponds to a particular goal pattern. When the attempt is queried, the system begins backward chaining, looking for goal-rules whose consequent pattern matches the attempt pattern.

After finding a matching pattern in the consequent of a goal-rule, sub-attempts are created from patterns in the antecedent of the goal-rule. These sub-attempts then activate rules in rule-sets which compare slot values of the stand instance (e.g. Flathead_01234) with required limitations depicted in the rule (i.e. whether conditions exist in the current stand for a good, moderate or poor residual stand and economic concerns when the proposed treatment is applied) (Fig. 5.6). During this process, mathematical algorithms are called to provide needed information. For example, the amount of board ft. which may be removed from a stand is based on the habitat type of the stand and the amount of harvested board ft. needed to be economically feasible. A message is sent to a Lisp function to calculate this value when the slot is accessed. If all constraints in the antecedent of the goal-rule are satisfied, the AND-THEN part of the rule is fired, asserting answers to slots in the Final-Report instance. Otherwise, the attempt fails and another attempt is queried.

There is one attempt for each treatment option, and because the Salvage and Sanitation Thin options contain 2 strategies each (see Table 5.2), a total of 6 treatment options are attempted. There are many goal-rules for each treatment however, one for each combination of the expected residual stand (good, moderate and poor) and economic concerns (good, moderate and poor). For example, the Regeneration Harvest option has 9 goal rules, 2 sets of 3 options (3^2). A total of 39 goals may be checked for each stand.

As each treatment option is queried and satisfied the results are written to an output file in DOS (Fig. 5.7) and to an output screen within Goldworks. More than one treatment may be prescribed for a single stand, and for each treatment chosen, the values for the residual stand and economic concerns are also reported. For example, Sanitation Salvage may be recommended with a moderate residual stand and good

economics, and a Sanitation Thin with poor residual stand and only moderate economics. The user may then choose the appropriate treatment based on their own knowledge and the additional information provided by the system.

Discussion

Currently, the interface between the user and system provides a means to input data, obtain a general description of the objectives of the system, and view a subset of the output. Many stands can quickly be run through the system, providing a summary report of the appropriate treatment options for each stand. This is useful as a time-saving feature for silviculturists who must write prescriptions for many stands. In addition to being an effective decision-making tool however, knowledge-based systems are also useful as tutorials. The reasoning behind a particular action may be acquired in the interview process, and then included in the system as explanations.

Justifications were obtained for components of the decision network during interviews with silviculturists. In the future, these will be included in a separate version of the system with a more enhanced user interface. This will provide silviculturists with an environment for learning about the prescription process on the Flathead National Forest when the MPB needs to be considered. Since U.S. Forest Service personnel are often transferred to new Forests, this will help to familiarize silviculturists from other areas with the interaction between LPP stands and the MPB on the Flathead.

Evaluation of a knowledge-based system and a simulation model are similar in that they both involve two distinct steps (Law and Kelton 1982, Plant and Stone 1991). Verification is determining whether the program performs as intended, (i.e. debugging the code). This process has been performed for the system. Each of the 39 goal-rules were tested by successively altering a dummy input data file, and making sure the

system fired the appropriate rules and found the appropriate treatment option. The other step, validation, is a more complex task. Validation requires checking to make sure the solutions provided by the system are an accurate representation of the human expert's knowledge which was used to build the knowledge-base. This task will be performed in the near future using stand data from the Flathead National Forest. As part of this process, the silviculturists who were initially interviewed for the knowledge-base will be consulted to identify gaps in the knowledge-base and verify the logic of the reasoning. Additional independent silviculturists will also be used in the validation process. In this type of system it is also important to evaluate the benefits, such as time and/or money saved, provided by the system. Performance of this aspect of the system will also be evaluated.

Conclusions

Forest Service personnel (both in Forest Pest Management (FPM) and at the District level) have often voiced concern about the need for useful and innovative improvements in data interpretation, and a more rapid implementation of new ideas from research. A knowledge-based system such as the one described in this paper will help in these tasks. Research on the MPB/LPP relationship has been ongoing for several decades, but the facts are often left unused. With this system, knowledge gained by research endeavors and a select few managers can be used by others encountering the same problems. It provides managers with a tool to help them with complicated decisions that were previously difficult to make due to a lack of adequate information. Updates to the system will also provide an efficient avenue for transfer of new knowledge about the MPB/LPP interaction. Biological information is very

important to this system however, and the computer should not be isolated from the forest.

The MPB Advisory System was originally designed to address routine situations encountered when making stand prescription decisions that are influenced by MPB populations. Stands with more complex circumstances are not yet included. Even though not all problems can be solved by this system, by speeding up the prescription writing process, it will provide silviculturists with more time to deal with stands that have special problems. The basic framework also furnishes a structure for easy incorporation of additional decision processes such as those needed for management objectives other than timber production. Although the targeted users of the system are silviculturists on National Forests in northern Montana, the modularity of the system also provides an interface to models which can be used by other resource managers. For example, addition of the MPB phenology model will provide FPM with a user friendly means to examine weather related MPB population trends. Since most Forest Service District offices now do not have PC compatible computers, delivery will ultimately be on the DG computer system.

Due to the many interacting elements in the MPB/LPP relationship, not all MPB problems can be predicted and/or prevented. This system, however, is a first step towards applying what we know about the complicated interactions between the MPB and LPP in a manner which can be more easily accessed. Silviculturists will benefit in many ways by the synthesis of information about MPB populations with economic and silvical characteristics of a stand. The probability of a widespread MPB outbreak may be reduced, in addition to the traditional benefits of silvicultural treatments. Including these considerations in the initial planning process will promote more efficient timber management aimed at meeting specific landuse objectives.

To alleviate widespread MPB outbreaks, it will be necessary to achieve a mosaic of age classes, species composition, and sizes of lodgepole pine stands over a large area (Cole, D.M. 1989). To realize these goals, resource managers will eventually need to take a holistic view of the problem and look beyond stand and forest boundaries. The spatial distribution of other stands and how they effect the stand under consideration, as well as the spatial distribution of MPB populations, are important components currently missing. Incorporating GIS capabilities will facilitate improvements in this area. For now however, implementation of the MPB Advisory System will provide a relatively simple method for integrating the complex tasks required in MPB and LPP management.

Table 5.1. United States Forest Service personnel interviewed during the knowledge acquisition process.

Dr. Gene Amman

Principle Entomologist

**Mountain Pine Beetle Population Dynamics Research Work Unit
Intermountain Research Station
Ogden, UT**

Mr. Paul Beckley

Forest Economist

**Flathead National Forest
Kalispell, MT**

Mr. Barry Bollenbacher

Silviculturist

**Swan Lake Ranger District
Flathead National Forest
Bigfork, MT**

Current Address:

**Butte Ranger District
Deerlodge National Forest
Butte, MT**

Mr. Dick Call

Zone Timber Staff Officer, retired

**Helena National Forest
Helena, MT**

Mr. Ken Gibson

Entomologist

**Timber, Cooperative Forestry and Pest Management
Missoula, MT**

Dr. Dick Schmitz

Principal Entomologist

**Mountain Pine Beetle Population Dynamics Research Work Unit
Intermountain Research Station
Ogden, UT**

Mr. Jim VanDenburg

Silviculturist

**Flathead National Forest
Kalispell, MT**

Table 5.2. Silvicultural treatment options identified in the knowledge acquisition process to be useful for reducing losses caused by the mountain pine beetle.

Salvage Cutting:	<p>The harvest of MPB induced mortality, or impending mortality due to the MPB. This treatment is often used in stands under attack by the MPB to reduce wood losses.</p> <ol style="list-style-type: none">1. Sanitation Salvage: remove both dead and susceptible green lodgepole pine.2. Salvage Dead LPP: remove only the dead lodgepole pine.
Sanitation Thinning:	<p>Provides a reduction of stand stocking to protect the residual stand from MPB population outbreaks while providing cover and aesthetics for other resource benefits. This treatment has also been referred to as Partial Cutting.</p> <ol style="list-style-type: none">1. Pre-commercial thin: Used mostly in recreational areas for aesthetic purposes.2. Commercial thin: Used in stands where the trees are large enough to provide economic benefits.
Regeneration Harvest:	<p>Stand replacing harvest (clearcutting).</p>
Defer:	<p>Delay any treatment in the stand until re-evaluation in the next planning phase.</p>
Pheromones:	<p>Semiochemicals used for manipulating MPB populations until silvicultural treatments may be applied, or in conjunction with certain treatments.</p> <ol style="list-style-type: none">1. Anti-aggregating: Used for dispersing populations.2. Aggregating: Used for containing a small infestation in a stand which is planned to be harvested in the near future

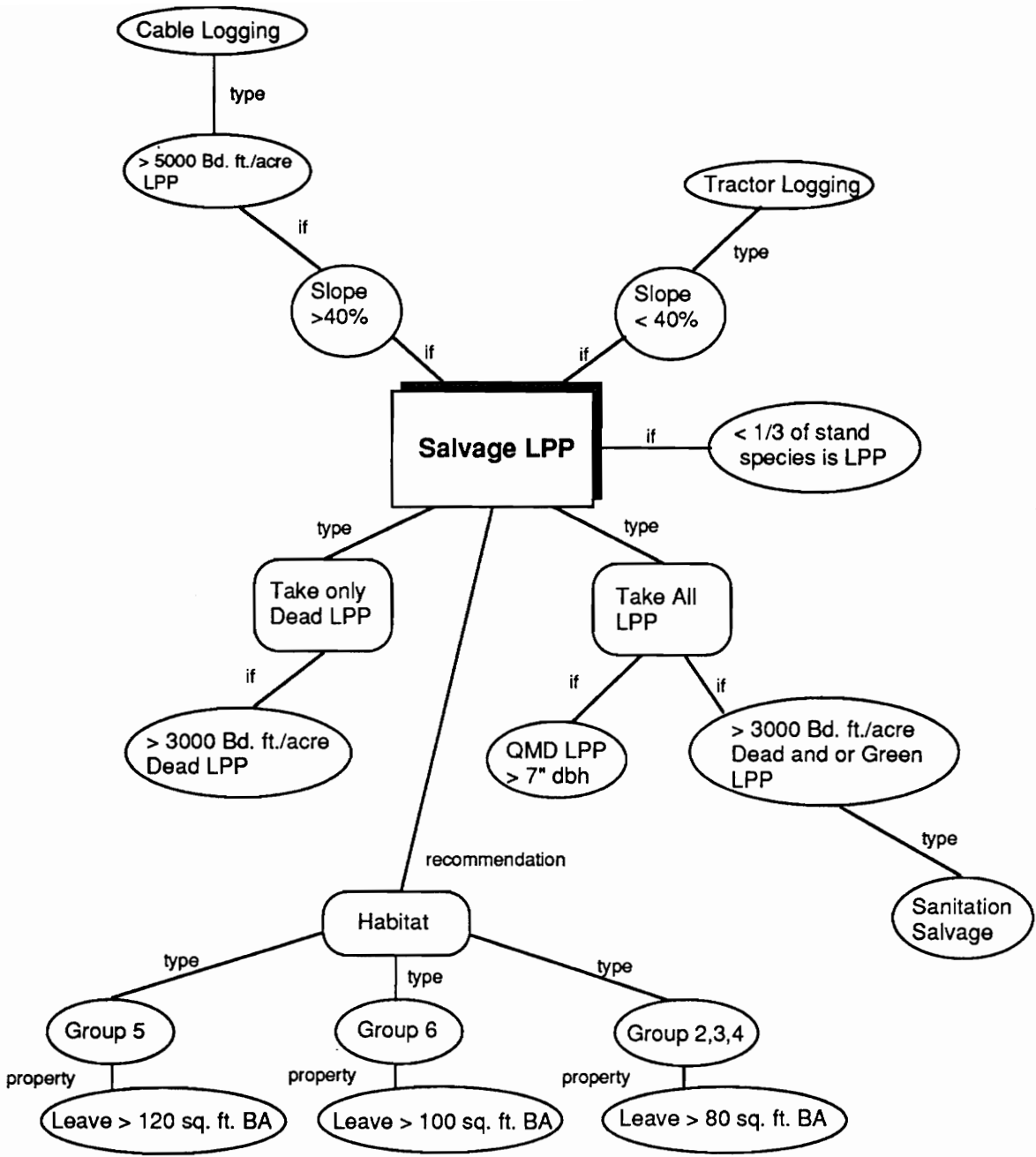
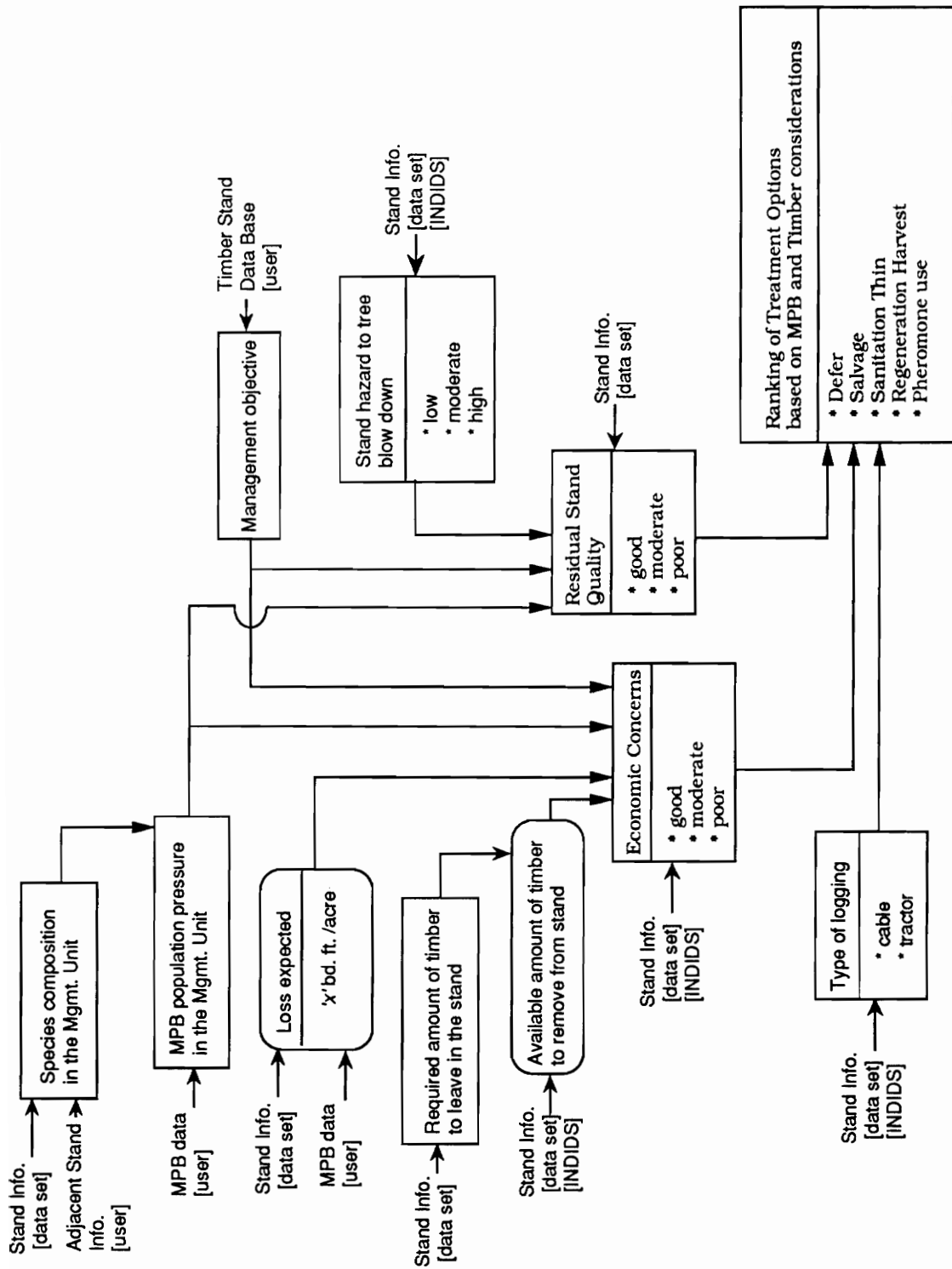


Figure 5.1. One section of the knowledge network graph representing the declarative knowledge of silviculturists on the Flathead National Forest. Each node is a concept or proposition describing some part of the stand prescription process. Nodes are linked by relations. LPP = lodgepole pine, QMD = quadratic mean diameter.

Figure 5.2. Function model of the decision process used in determining silviculture treatments for lodgepole pine stands when the mountain pine beetle is an influencing factor. Each box describes a separate decision which must be made before determining the overall goal, the optimal silvicultural treatment option. Rounded boxes represent decisions which are solved using quantitative models, and square boxes have rule-bases associated with them. Information flow required for each decision is represented by arrows.



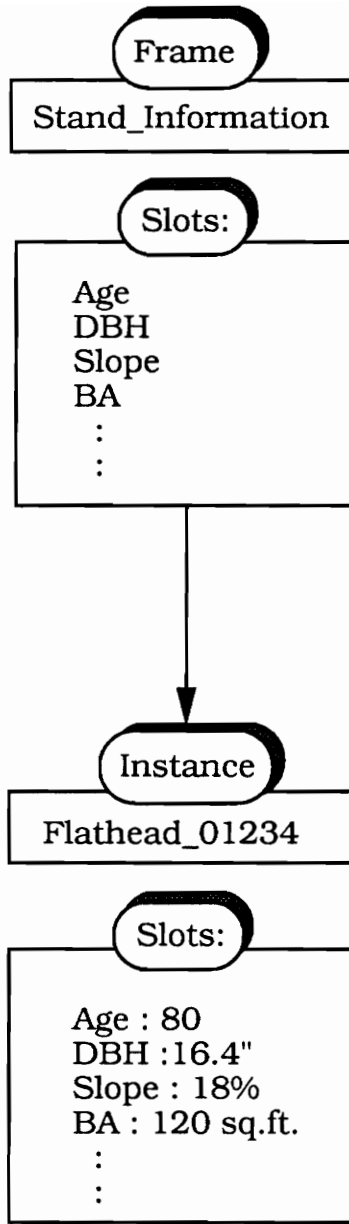


Figure 5.3. An example of the frame-based knowledge structure used in the MPB Advisory System. A frame is used to describe a general class of objects, such as Stand_Information. Flathead_01234 is a specific instance of Stand_Information with slot values which store specific data pertaining to the stand.

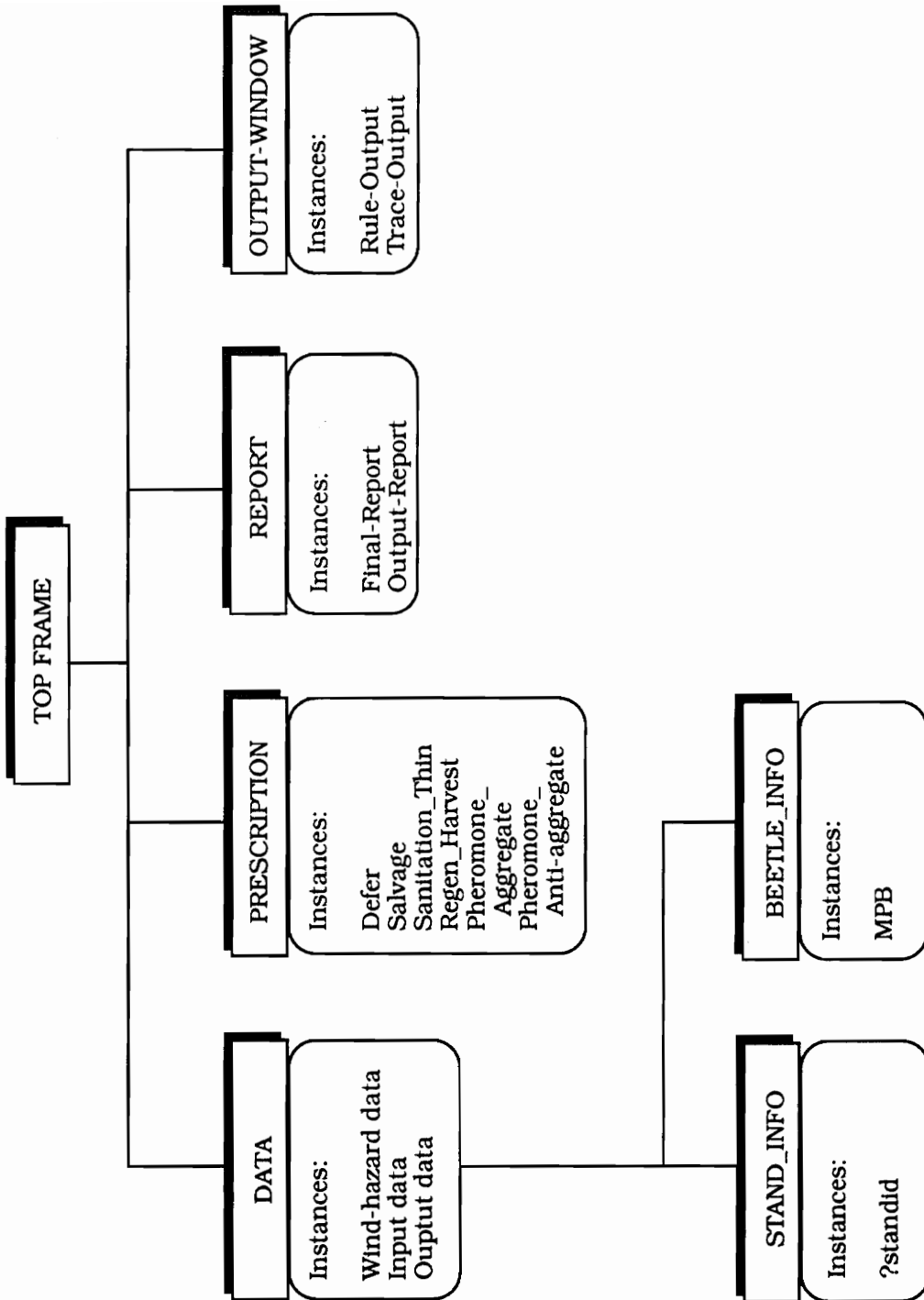


Figure 5.4. Hierarchical frame structure for the MPB Advisory System. Each box represents a frame and the associated instances with that frame. Top Frame is a Goldworks system structure inherent in all applications developed with this software. ?name' symbolizes a variable.

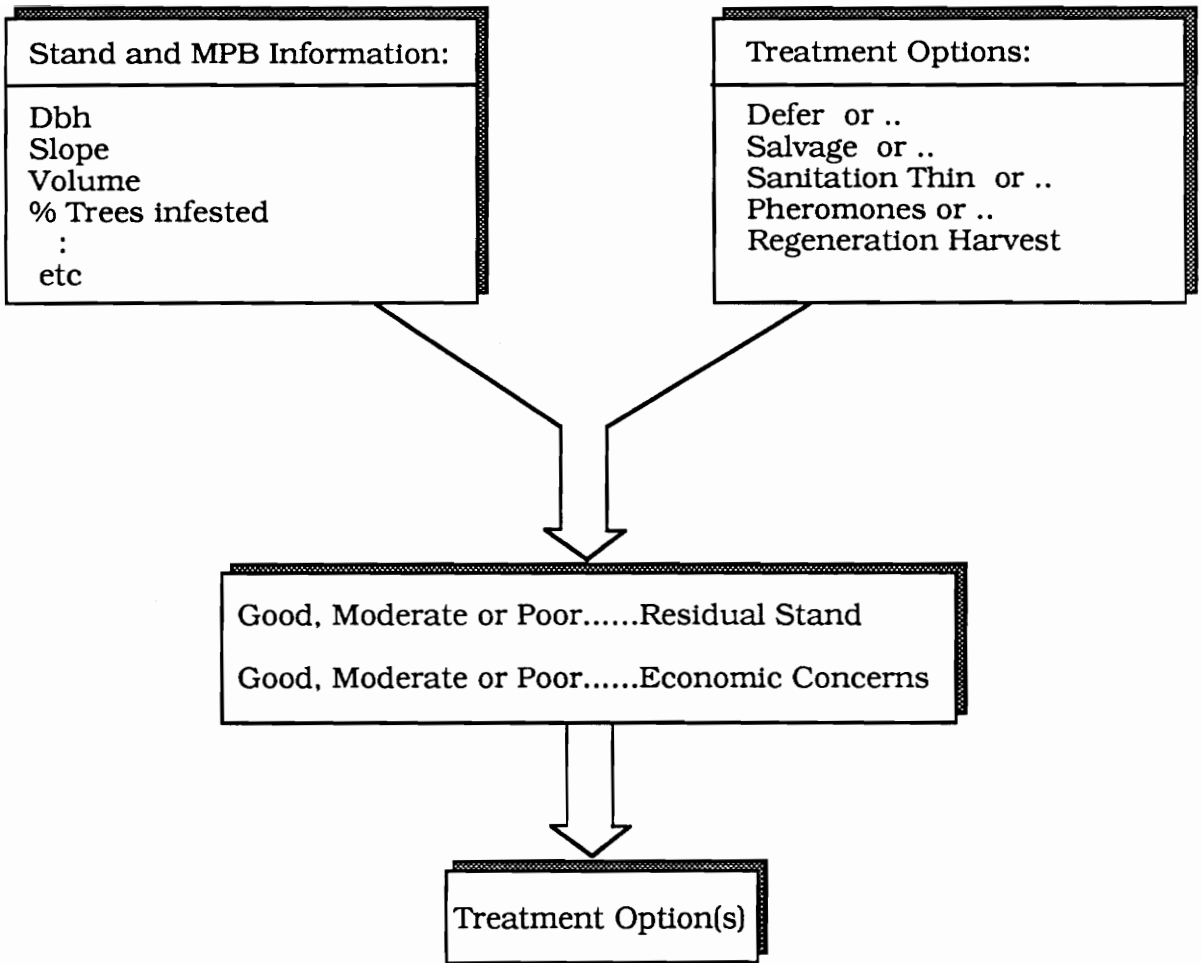


Figure 5.5. Knowledge structure of the rule-base. Stand and MPB population information, and treatment option are used to estimate the quality of the residual stand and economic concerns. The optimal treatment provides the best (Good) of both constraints.

Figure 5.6. Example of the reasoning structure for the Regeneration Harvest treatment option. Rules shown are for 'good' residual stand and 'good' economic concerns only. When the attempt is queried, the backward-chaining goal-rule searches for a pattern to match each part of the rule consequent. The enabling pattern in the Rule-Sets match these patterns, and rules within the sets are then fired. If these rules are satisfied, control is sent back to the goal-rule and the AND-THEN part of this rule is fired, resulting in the answer being placed in slots of the final-report instance.

Attempt Definition:

```
(setq regen (make-attempt '(instance regen_harvest is prescription
                               with economics ?oeco3
                               with resid_stand ?ocond3
                               with strategy not-an-option)))
```

Attempt Query:

```
(Query-all regen)
```

Goal-Rule:

```
(DEFINE-RULE goal-regen-all-best
 (:direction :backward)
 (instance regen_harvest is prescription
            with resid_stand good
            with economics good)
 THEN
 (instance regen_harvest is prescription
            with economics good
            with resid_stand good
            with strategy not-an-option)
 AND-THEN
 (instance final-report is report
            with prescript_rpt regen_harvest
            with resid_rpt rh-good
            with econo_rpt rh-good))
```

Rule Sets:

```
(DEFINE-RULE-SET regen-eco ( )
 (economics regen_harvest ?reco)
```

```
(DEFINE-RULE regen_harvest-
economics-good
 (:direction :forward)
 (instance ?standid is stand_info
            with loss_predicted ?loss)
 (>= ?loss 5000)
 (Instance regen_harvest is
 prescription)
 THEN
 (instance regen_harvest is
 prescription
            with economics good)))
```

```
(DEFINE-RULE-SET regen-resid ( )
 (resid_stand regen_harvest ?rrs)
```

```
(DEFINE-RULE regen_harvest-
resid_stand-good
 (:direction :forward)
 (instance ?standid is stand_info
            with age_lpp ?age
            with ba_remaining_stand ?ba)
 (>= ?age 80) (<= ?ba 150)
 (instance regen_harvest is
 prescription)
 THEN
 (instance regen_harvest is
 prescription
            with resid_stand good)))
```

* Mountain Pine Beetle Advisory System *
* Summary Report *

Date: 08/23/91
Forest: FLATHEAD
Stand: 1234

Stand Information:

Current stand Basal Area: 250 sq.ft.
Loss expected over 10 years: 11000 bd.ft.
Remaining stand Basal Area: 125 sq.ft.
Hazard to tree blow down: LOW

Taking into account the Mountain pine beetle, the following treatments are recommended for this stand. Reported with each treatment option are the qualitative values for corresponding components (Good, Moderate or Poor).

1) Salvage Dead LPP:

Economic considerations are Good
Residual stand considerations are Moderate
For this habitat type, it is recommended to leave at least
80 sq. ft. BA in species other than lodgepole pine
This option is ideal for stands where cover for wildlife is needed
Cable Logging is recommended due to the slope
Economic considerations for cable logging are Moderate

2) Regeneration Harvest:

Economic considerations are Moderate
Residual stand considerations are Good

Aggregating pheromones may also be used in this stand in conjunction with one of the treatment options to manipulate MPB populations.

Figure 5.7. Example summary output file from the MPB Advisory system. Output is for hypothetical stand '1234' on the Flathead National Forest.

Conclusions

The preceding chapters describe aspects of the dynamic relationship between mountain pine beetle (MPB) populations and lodgepole pine (LPP) stands. Each chapter describes a particular component of an advisory system for managing LPP stands when the MPB is an influencing factor. The system is designed to be used for determining an appropriate silvicultural treatment for a LPP stand that is within the climatic zone of the MPB. Each component of the system fulfills a specific task in the stand management process. I will briefly summarize each chapter and describe how the component fits into the advisory system.

The phenology model discussed in Chapter 2 describes the temperature-dependent development of six life-stages of the MPB. The developed model was used to test specific life-history strategies relating to synchrony of adult MPB emergence. Model predictions using phloem temperatures from infested trees suggest that each life-stage has a unique development curve and temperature threshold which dictate moults to the next life-stage. These temperature-based restrictions throughout the year tend to synchronize the life-stages such that eventual adult emergence occurs relatively simultaneously. When many adult beetles emerge to attack new host trees at the same time, the defenses of the trees will more likely be overcome resulting in an increase in MPB population growth for the next year.

The phenology model also has utility in the stand management process. Using current temperature records to drive the model, a population decrease or increase the next year can be predicted. For example, temperature records from the fall and winter of the current year can be used in the spring to predict over-wintering mortality.

Results from these predictions will give an indication of adult emergence the following August. Averaged temperature records from preceding years could also be used to predict typical beetle development in the upcoming years. Predictions from the model would provide a general trend of the population, not absolute beetle numbers.

In light of several risk classification methods, the confusing terminology in MPB hazard and risk rating was discussed in Chapter 3. None of the methods evaluated, using stand data from three National Forests in northern Montana, were found to adequately predict stand risk to the MPB. An additional method based on a logistic regression was developed in attempt to improve predictions. This method also proved inadequate. Poor predictions from these methods are most likely due to unexplainable phenomena in the MPB/LPP system and also because of the two-phase nature of MPB populations. Endemic and epidemic populations behave differently, and consequently have different influences on a stand. Therefore, different factors are needed to describe the two separate phases. Because the mechanisms which trigger the transition from the endemic to epidemic phase are not fully understood, we are unable to predict the behavior of this phase. However, because a larger information base is available for epidemic population behavior, we may be more able to estimate the influence of this population phase on LPP stands. The distinction between the two populations types was not recognized in the methods evaluated. Additionally, there are many important factors such as the beetle population which are not included by simply measuring trees in a stand.

In Chapter 3, stand susceptibility was defined as the ability of a stand to sustain an outbreak beetle population, and risk as the likelihood of an outbreak population occurring in a stand. Risk includes a measure of both susceptibility and the MPB population. One approach to synthesize these two concepts is a model which

predicts the probability of a tree becoming infested based on susceptibility and MPB population pressure. Chapter 4 describes the development of an empirical simulation model for this purpose. The simulation model uses stand and tree characteristics, and a measure of the beetle population pressure, to predict tree infestation and subsequent mortality through time. Tree death is described by the logistic probability distribution. The simulation model can be used by managers for estimating the amount of timber loss a stand will sustain if an MPB outbreak were to occur. This information is useful in prioritizing stands for treatment and also in determining the appropriate treatment.

Knowledge which represents the stand management process for LPP when the MPB is an influencing factor was acquired from silviculturists in northern Montana. A knowledge-based system, the MPB Advisory System, was developed from this information (Chapter 5). The MPB Advisory System links qualitative information, in the form of rules, with model output and stand survey data. The major objective of the system is to provide silvicultural treatment options for a particular stand. Treatment options are chosen based on stand and site characteristics, and information concerning MPB populations. Output from a model similar to the one described in Chapter 4 is currently accessed by the system (Cole, W.E. and McGregor 1983) because that is the model now used by the silviculturists who were interviewed. Validation and a sensitivity analysis of the advisory system using output from both the Cole model and the simulation model described in Chapter 4 is needed to determine the appropriate model to be included in the system.

Development of the MPB Advisory System is ongoing and proposed additions are depicted in Figure C.1. Refer back to the function model in Chapter 5 (Fig. 5.2) for a detailed description of current decisions made in the MPB Advisory System. Ideally, the first decision that should be made is whether the stand being analyzed is in a high

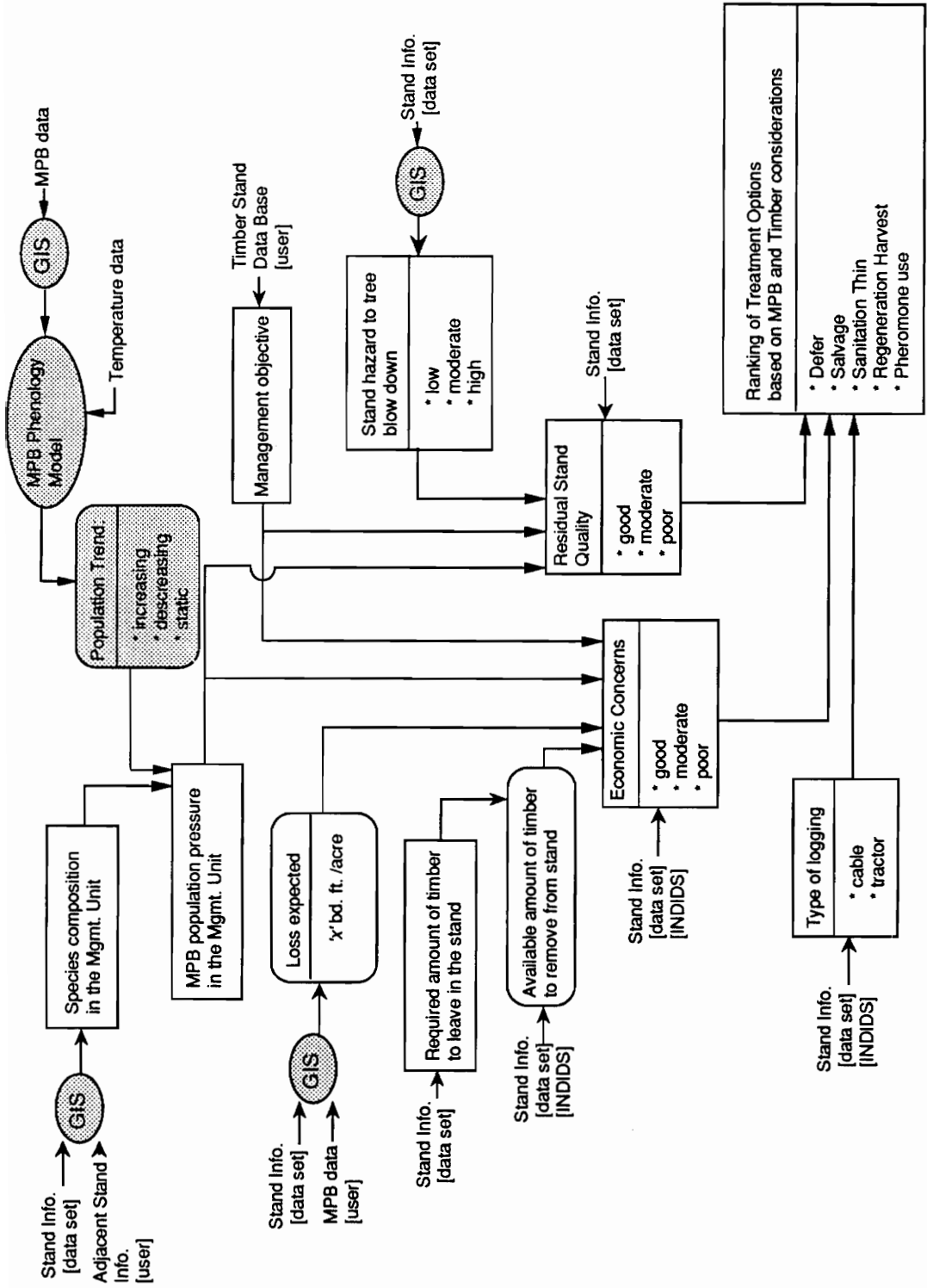
or moderate risk climatic zone. This rating could be based on the latitude and elevation of the stand, and would be similar in context to the Amman et al. (1977) risk classification method described in Chapter 3. MPB outbreak populations do not occur in certain climatic zones, and therefore there is no need to use the Advisory system for those stands.

Because decisions concerning management of forest ecosystems include information which is spatially distributed in heterogeneous landscapes, Geographic Information Systems (GIS) are also useful tools. A GIS could provide information concerning the spatial nature of both the stands and the beetle population in the management unit. Because beetle populations do not recognize stand boundaries, spatial information from surrounding stands is needed for a more accurate measure of the MPB population pressure.

As described previously, the phenology model could be used to determine the population trend, on either a long or short term basis. Knowledge of the population trend in the management unit could also help in determining the MPB population pressure influencing the stand.

The MPB Advisory System was designed to be used by U.S. Forest Service Silviculturists and FPM personnel. Presently, the system makes decisions necessary for determining the appropriate silvicultural treatment for LPP stands when timber production is the management objective and MPB populations are an influencing factor. Further development of a knowledge-base for using semiochemicals in the management process is needed. This system may be used in efforts to maintain the balance between LPP stands and MPB populations, while remaining within the bounds of prudent forest management.

Figure C.1. Proposed additions to the MPB Advisory System. Additional components which would increase the efficiency and predictive capabilities of the decisions currently made by the system are shaded grey. Circles represent external models accessed by the system. Refer to Figure 5.2 for a detailed description of the existing function model.



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Appendix I

Standardized residuals,

$$\frac{(observed - predicted)}{\sqrt{predicted(1 - predicted)}}$$

as a function of each explanatory variable used in the logistic regression models.

Figures A.1 - A.4 are for the regression model in Chapter 3:

- Figure A.1: Pooled for all Forests
- Figure A.2: Flathead National Forest
- Figure A.3: Kootenai National Forest
- Figure A.4: Lolo National Forest

Figures A.5 - A.40 are for the regression model in Chapter 4:

- Figures A.5 - A.20: By Stand
- Figures A.21 - A.40: By Diameter Class

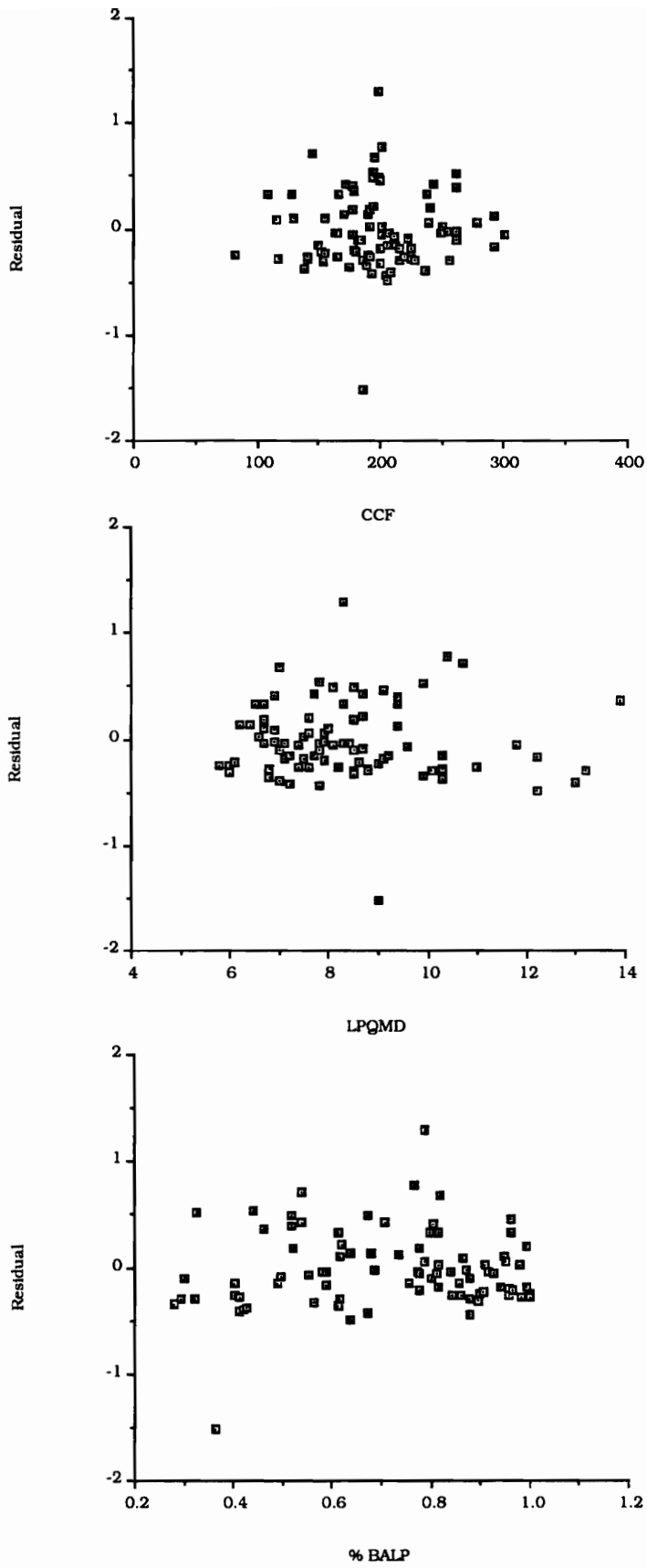


Figure A.1

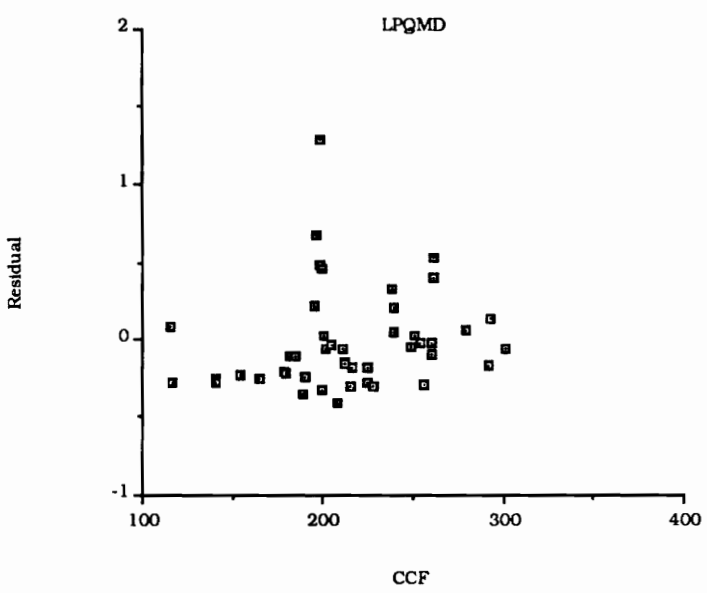
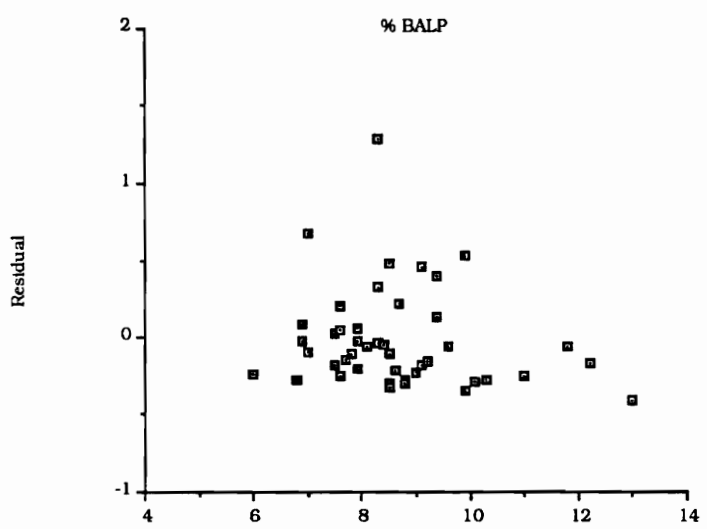
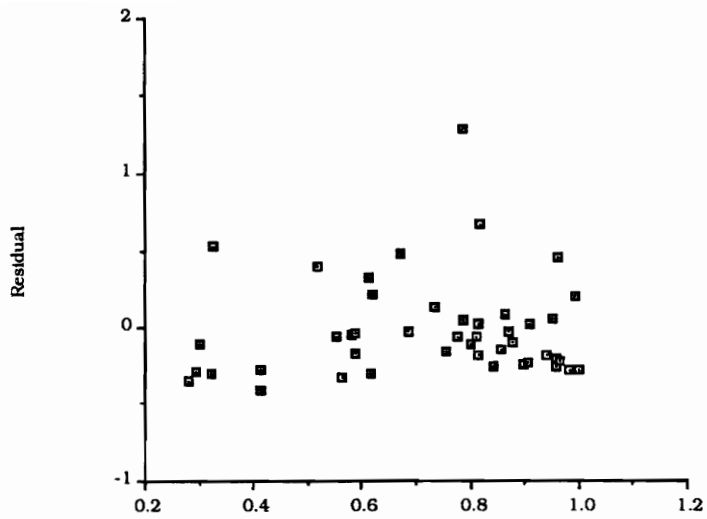


Figure A.2

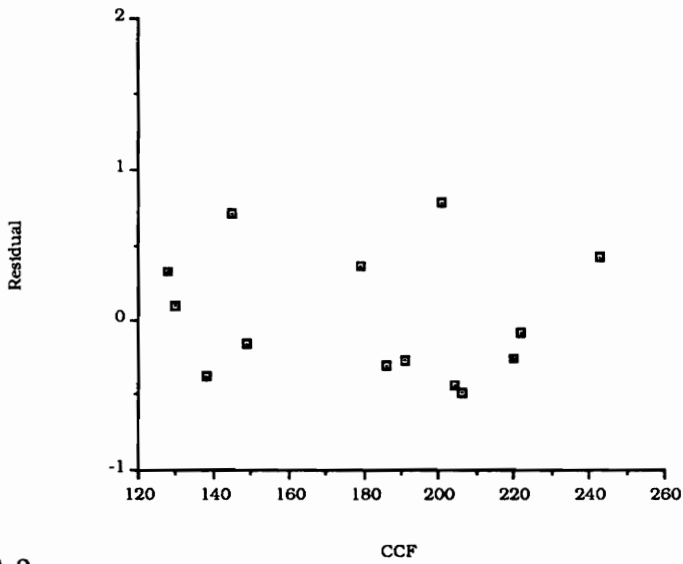
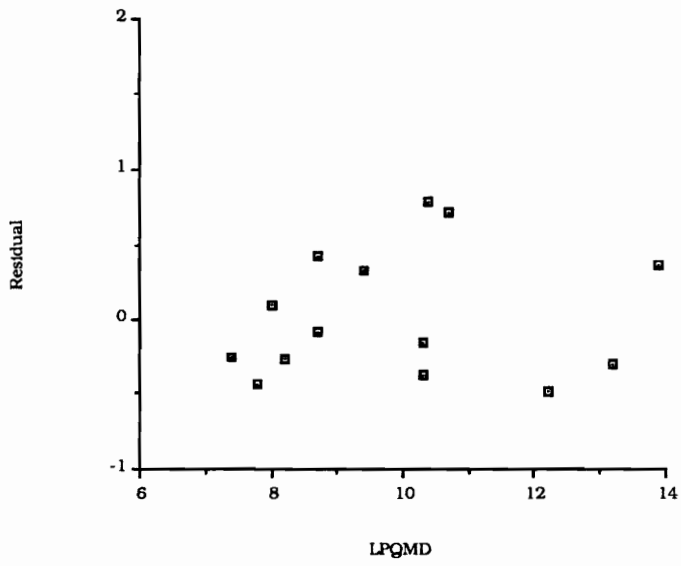
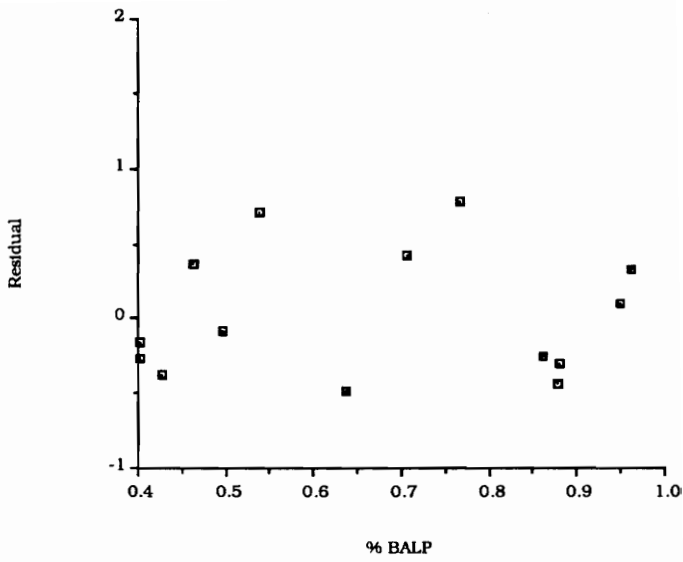


Figure A.3

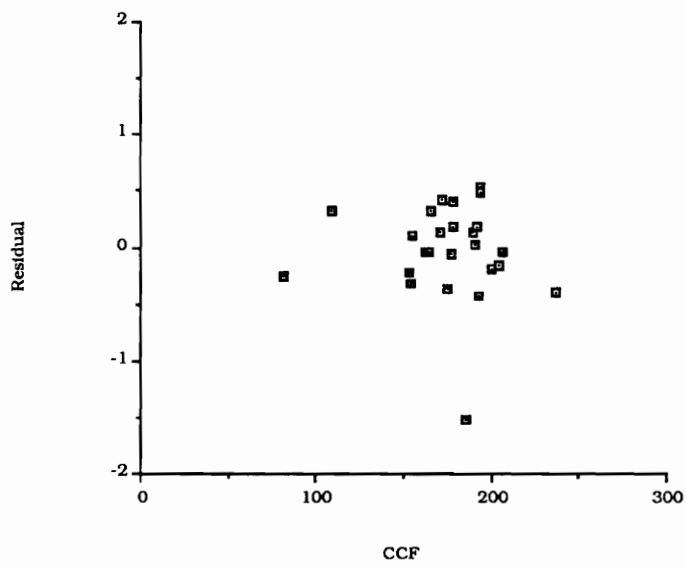
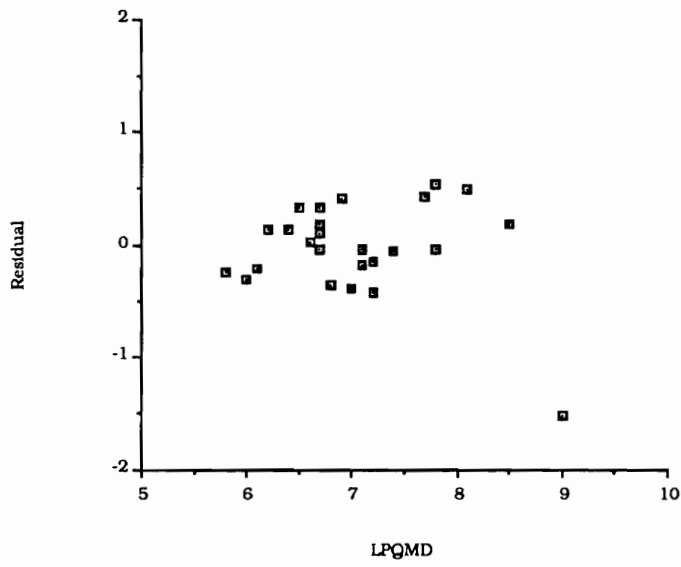
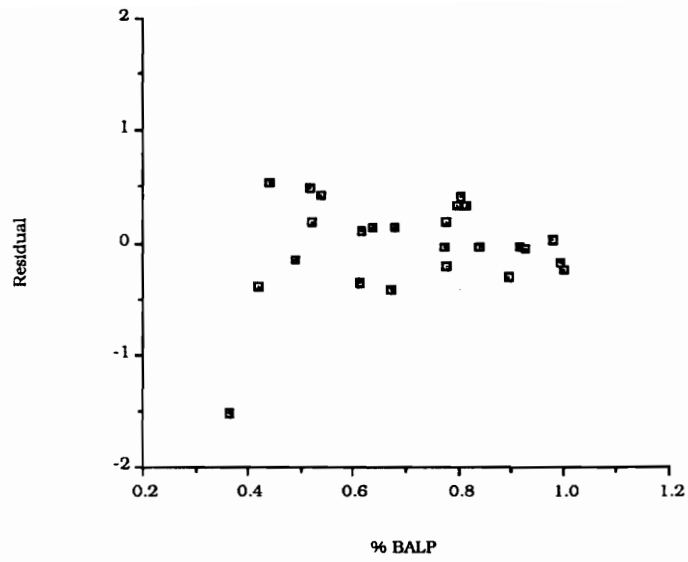
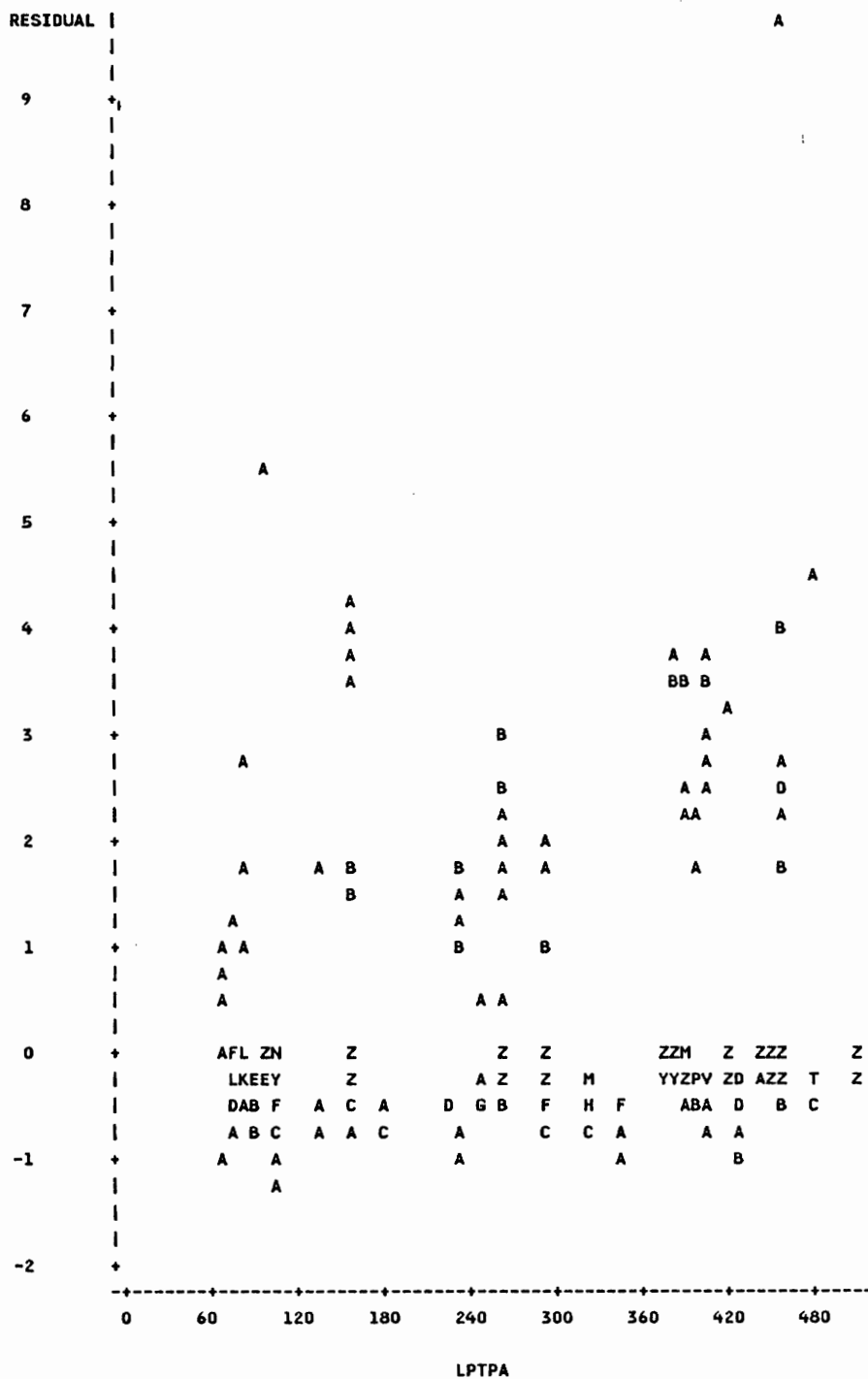


Figure A.4

STAND=1

PLOT OF RESIDUAL*LPTPA LEGEND: A = 1 OBS, B = 2 OBS, ETC.

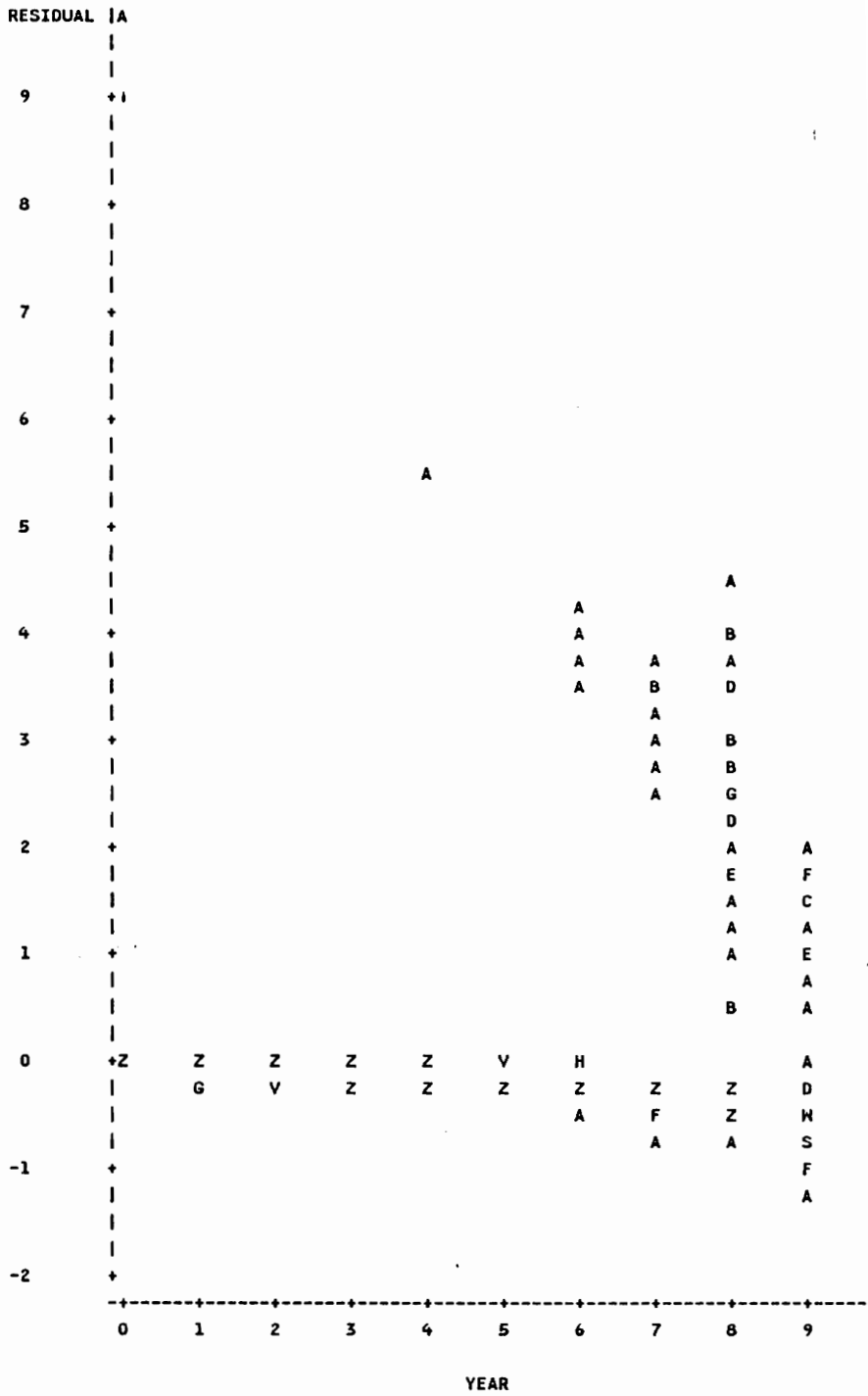


NOTE: 302 OBS HIDDEN

Figure A.5.

STAND=1

PLOT OF RESIDUAL*YEAR LEGEND: A = 1 OBS, B = 2 OBS, ETC.

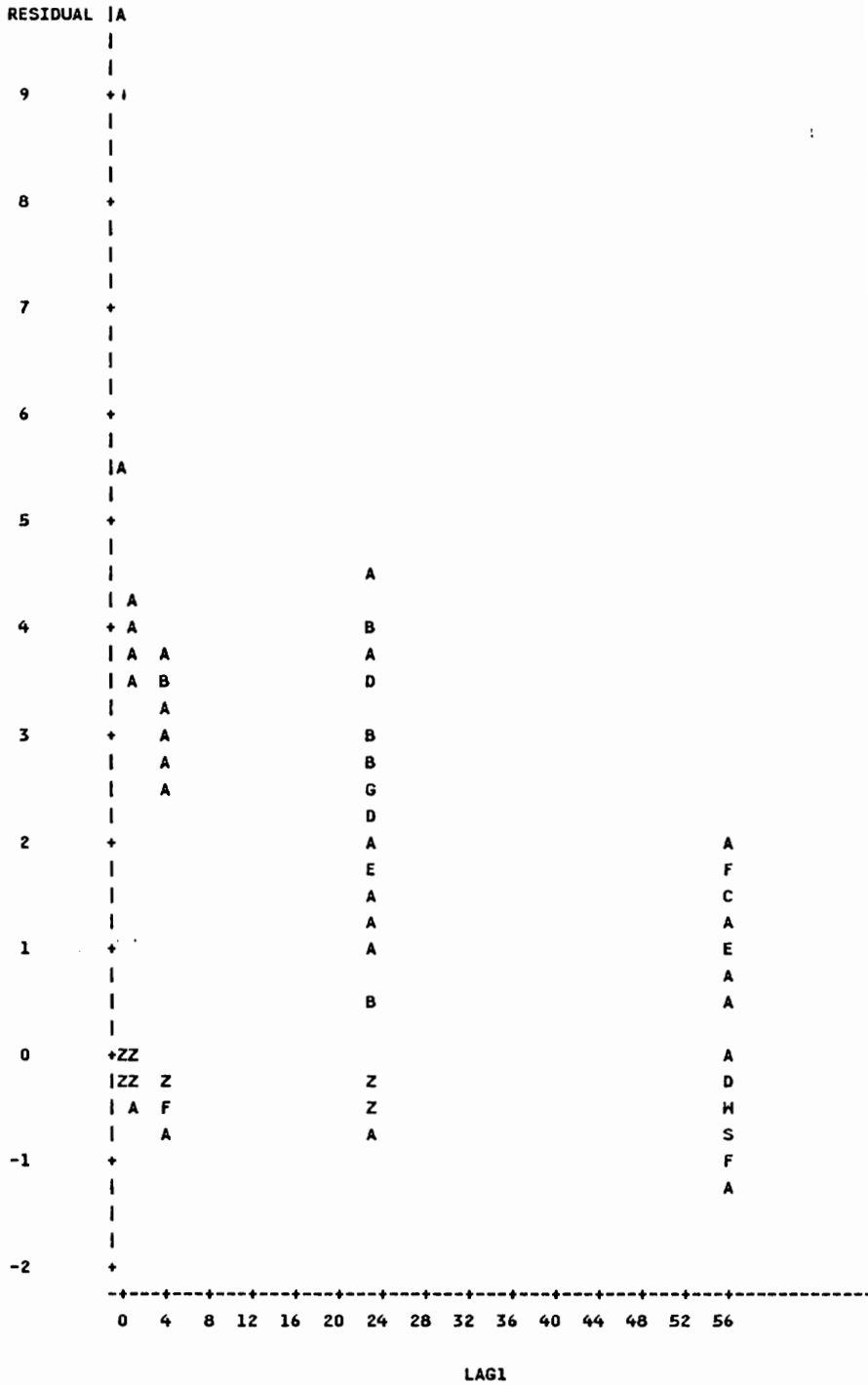


NOTE: 685 OBS HIDDEN

Figure A.7.

STAND=1

PLOT OF RESIDUAL*LAG1 LEGEND: A = 1 OBS, B = 2 OBS, ETC.

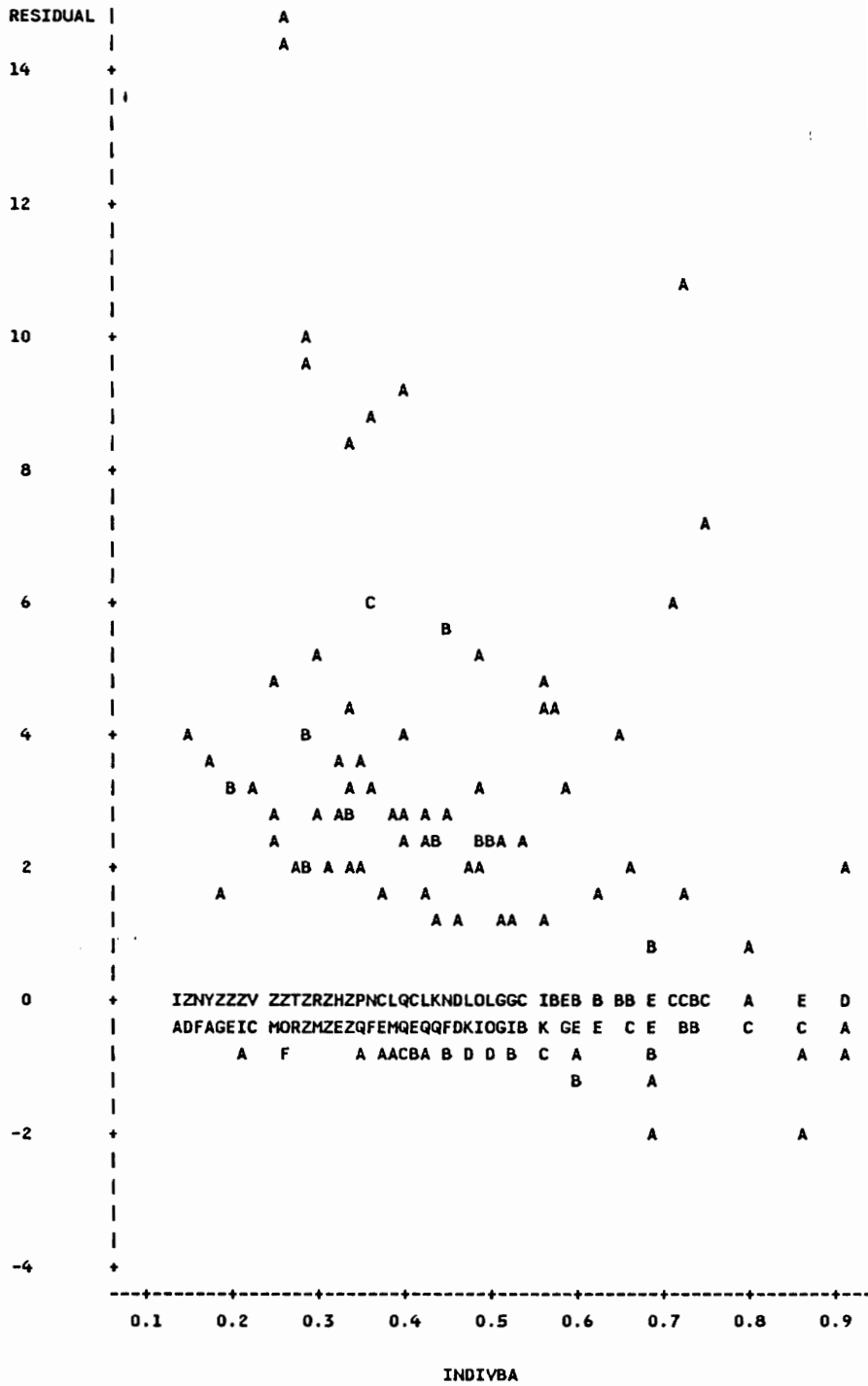


NOTE: 874 OBS HIDDEN

Figure A.8.

STAND=2

PLOT OF RESIDUAL*INDIVBA LEGEND: A = 1 OBS, B = 2 OBS, ETC.

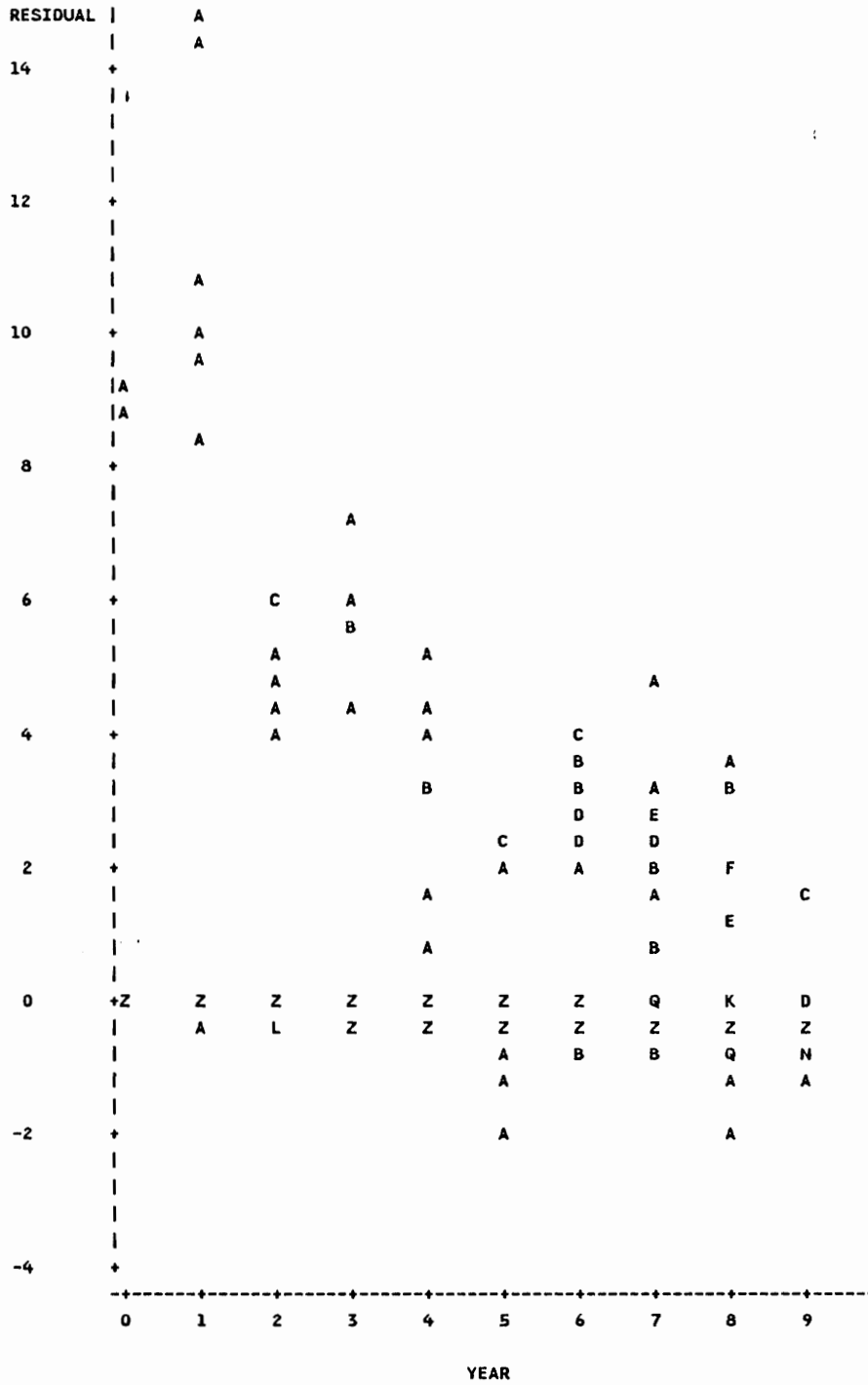


NOTE: 124 OBS HIDDEN

Figure A.10.

STAND=2

PLOT OF RESIDUAL*YEAR LEGEND: A = 1 OBS, B = 2 OBS, ETC.



NOTE: 662 OBS HIDDEN

Figure A.11.

STAND=2

PLOT OF RESIDUAL*LAG1

LEGEND: A = 1 OBS, B = 2 OBS, ETC.

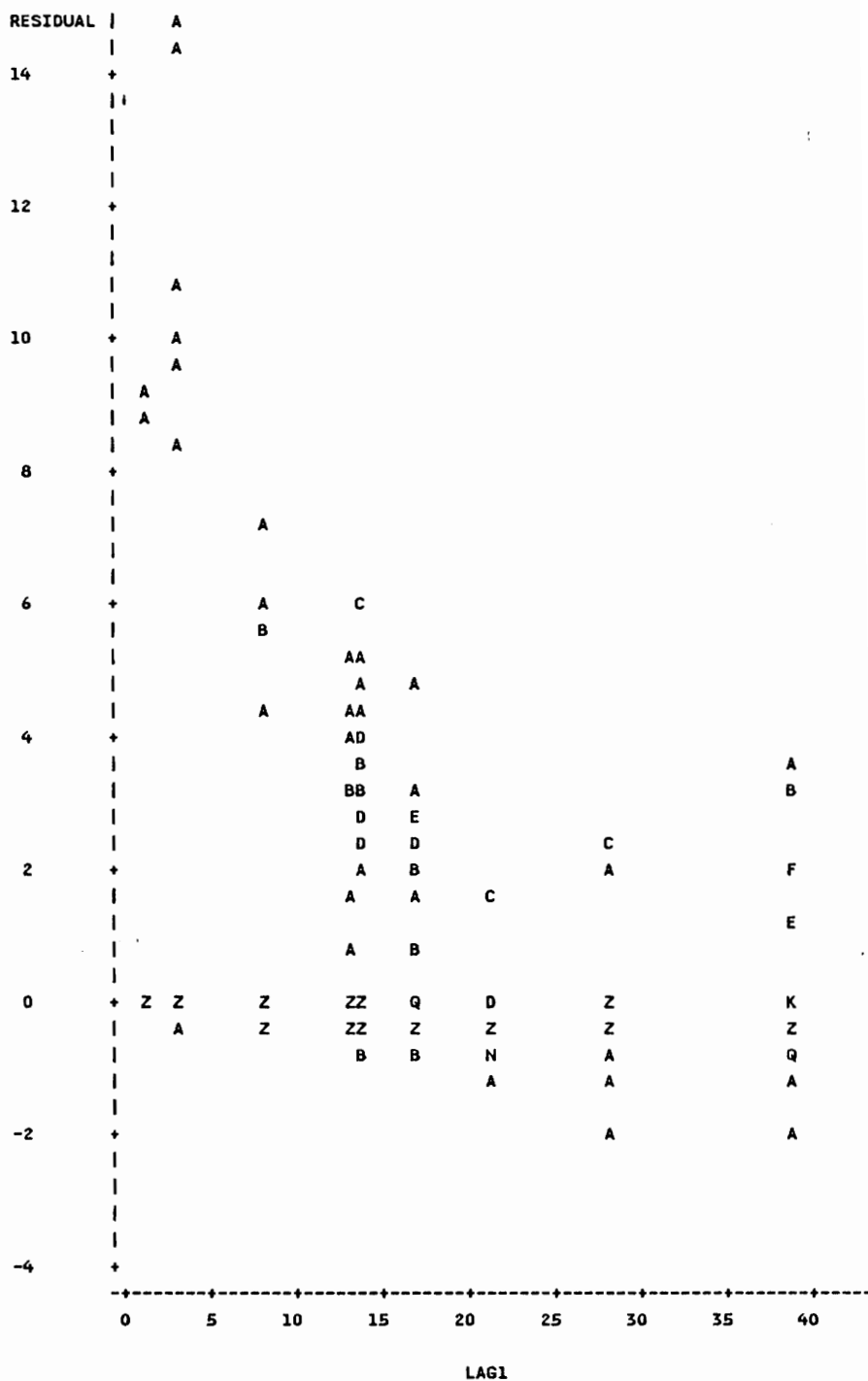
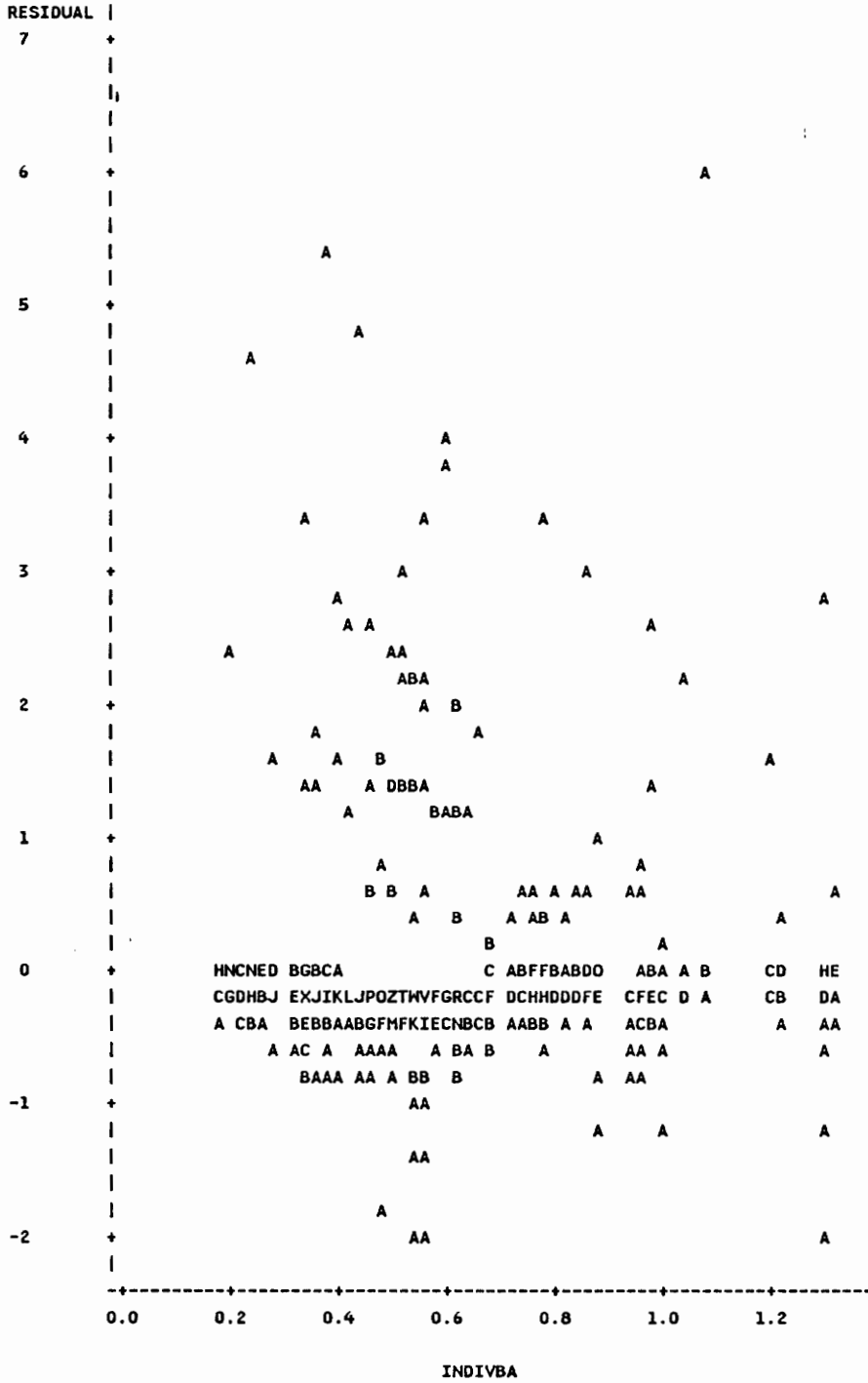


Figure A.12.

STAND=3

PLOT OF RESIDUAL*INDIVBA LEGEND: A = 1 OBS, B = 2 OBS, ETC.

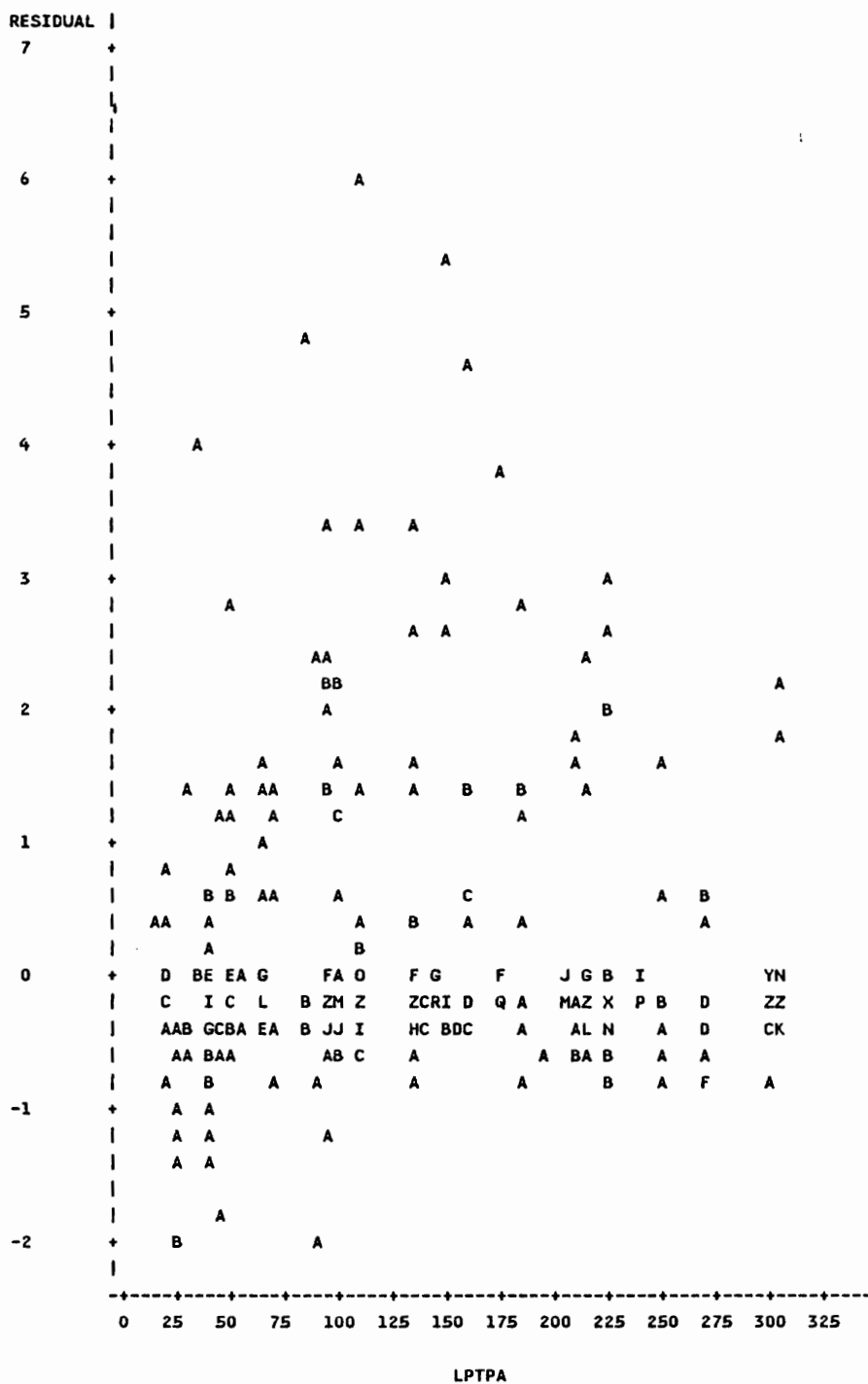


NOTE: 4 OBS HIDDEN

Figure A.13.

STAND=3

PLOT OF RESIDUAL*LPTPA LEGEND: A = 1 OBS, B = 2 OBS, ETC.



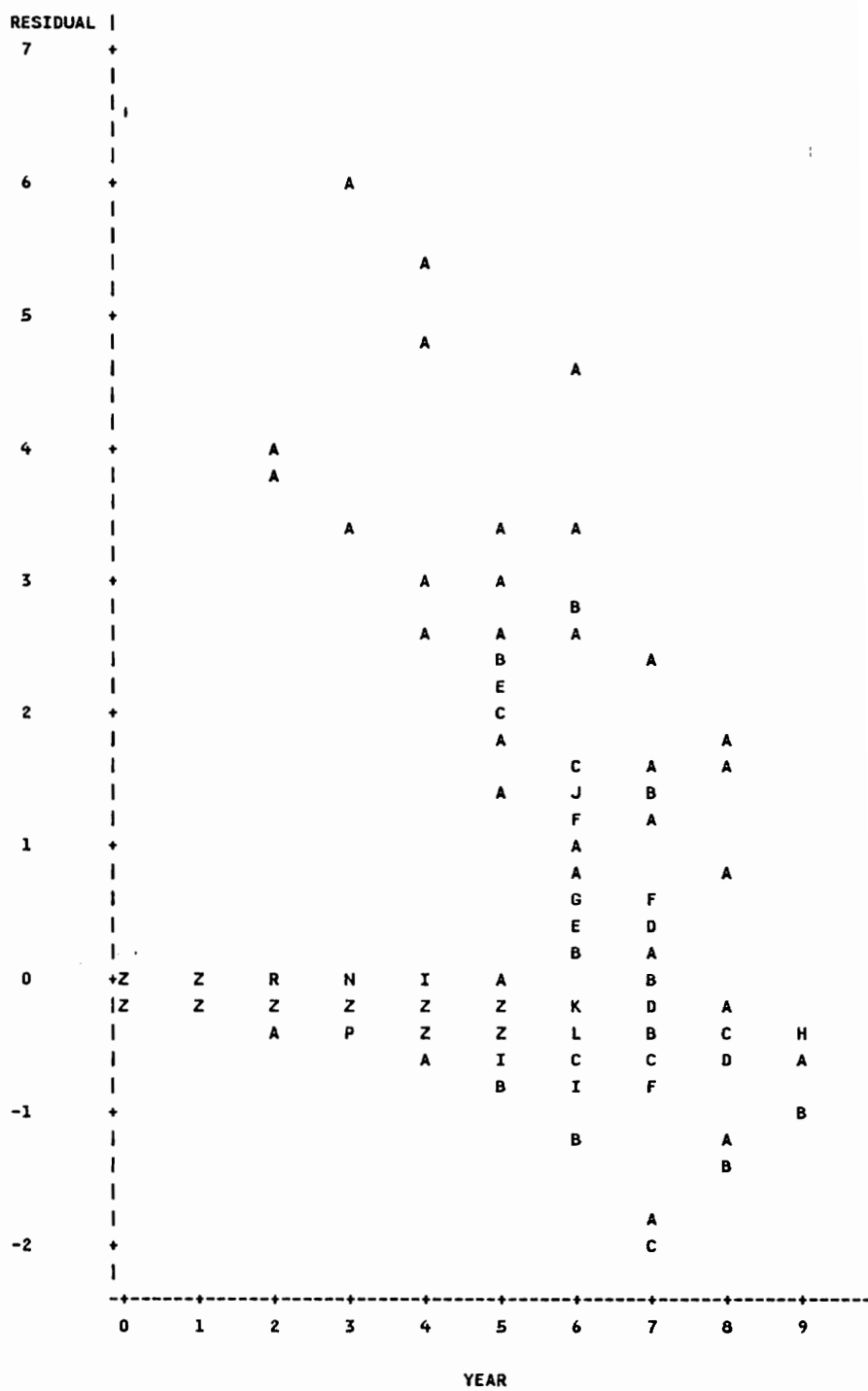
NOTE: 52 OBS HIDDEN

Figure A.14.

STAND=3

PLOT OF RESIDUAL*YEAR

LEGEND: A = 1 OBS, B = 2 OBS, ETC.



NOTE: 253 OBS HIDDEN

Figure A.15.

STAND=3

PLOT OF RESIDUAL*LAG1 LEGEND: A = 1 OBS, B = 2 OBS, ETC.

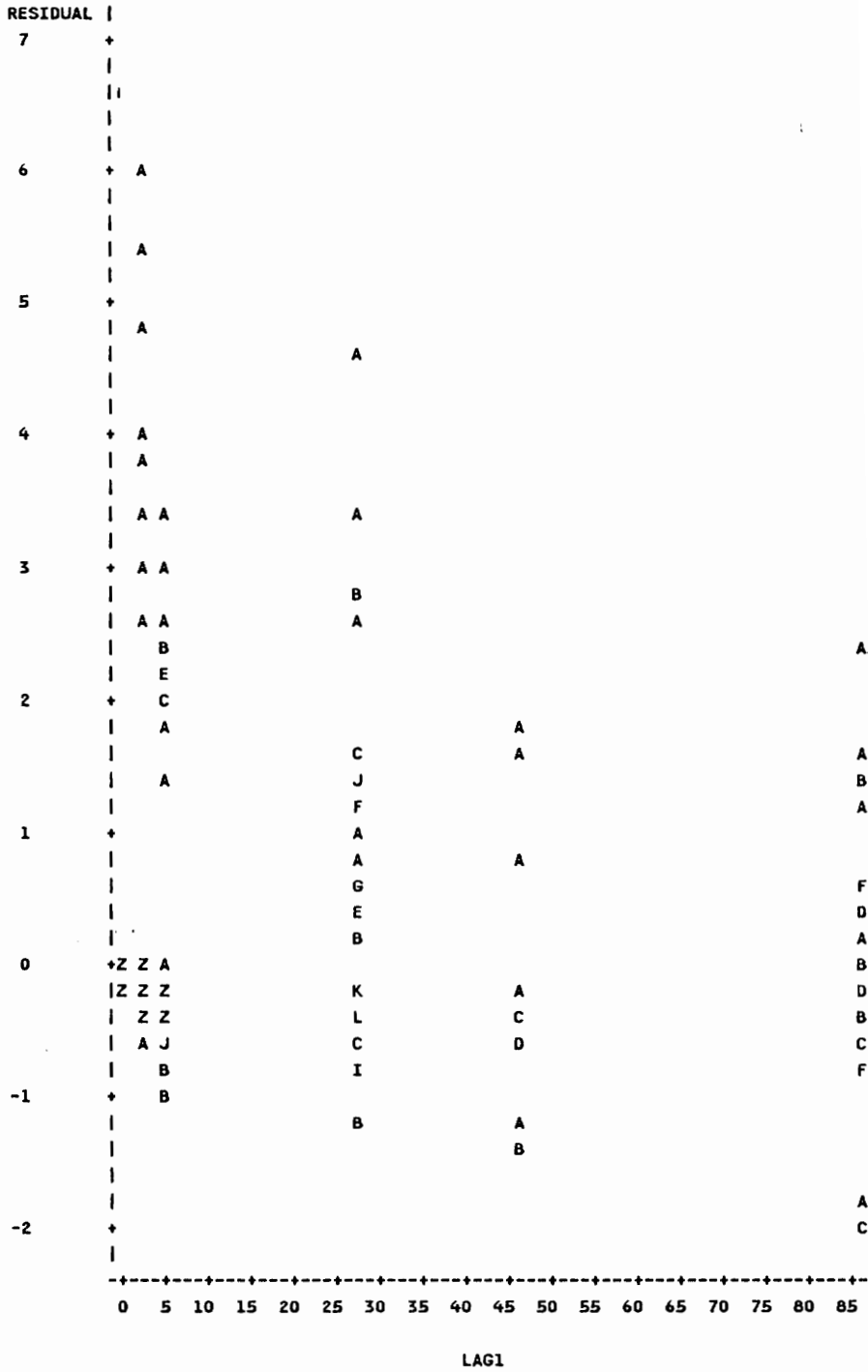
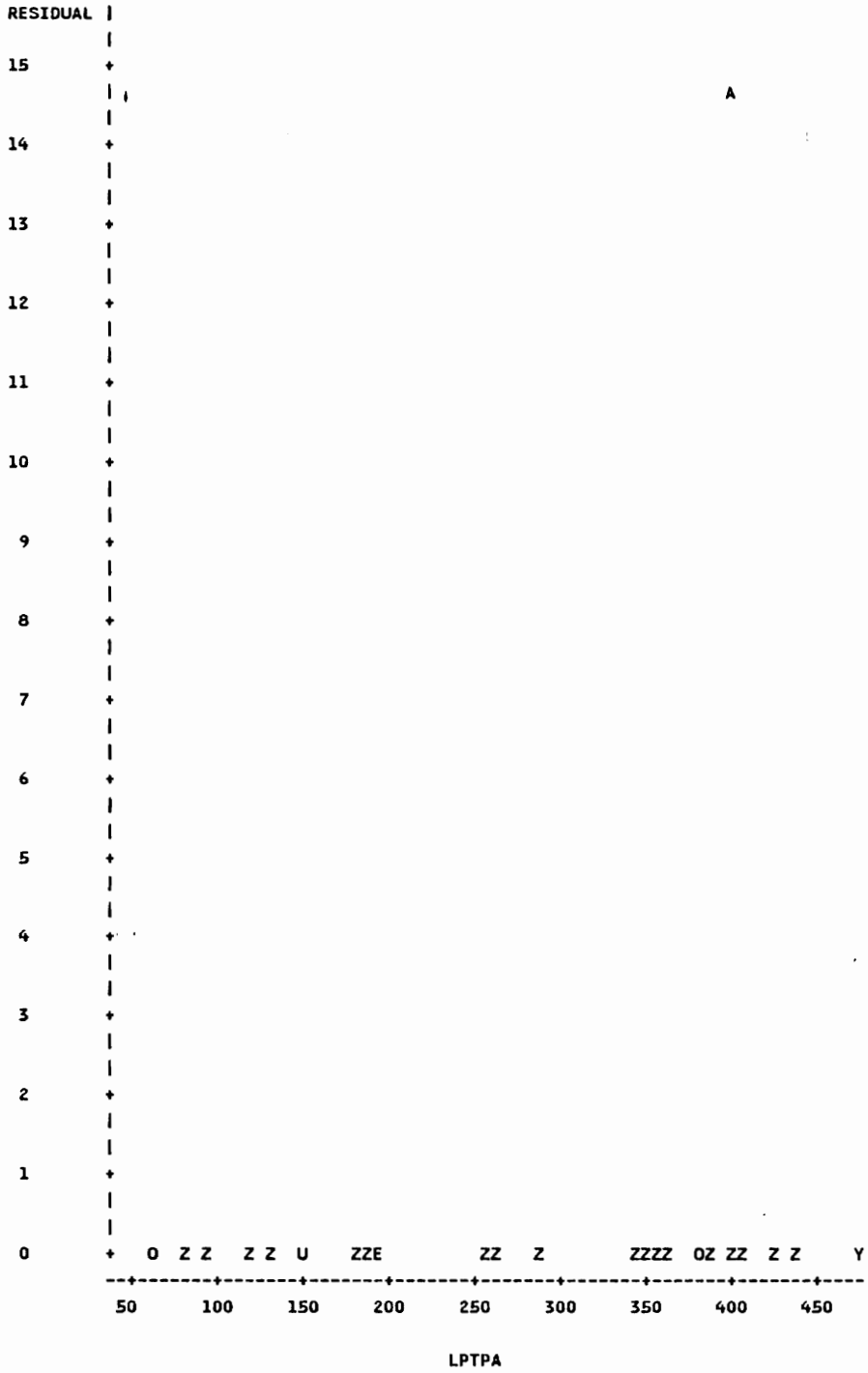


Figure A.16.

STAND=4

PLOT OF RESIDUAL*LPTPA

LEGEND: A = 1 OBS, B = 2 OBS, ETC.

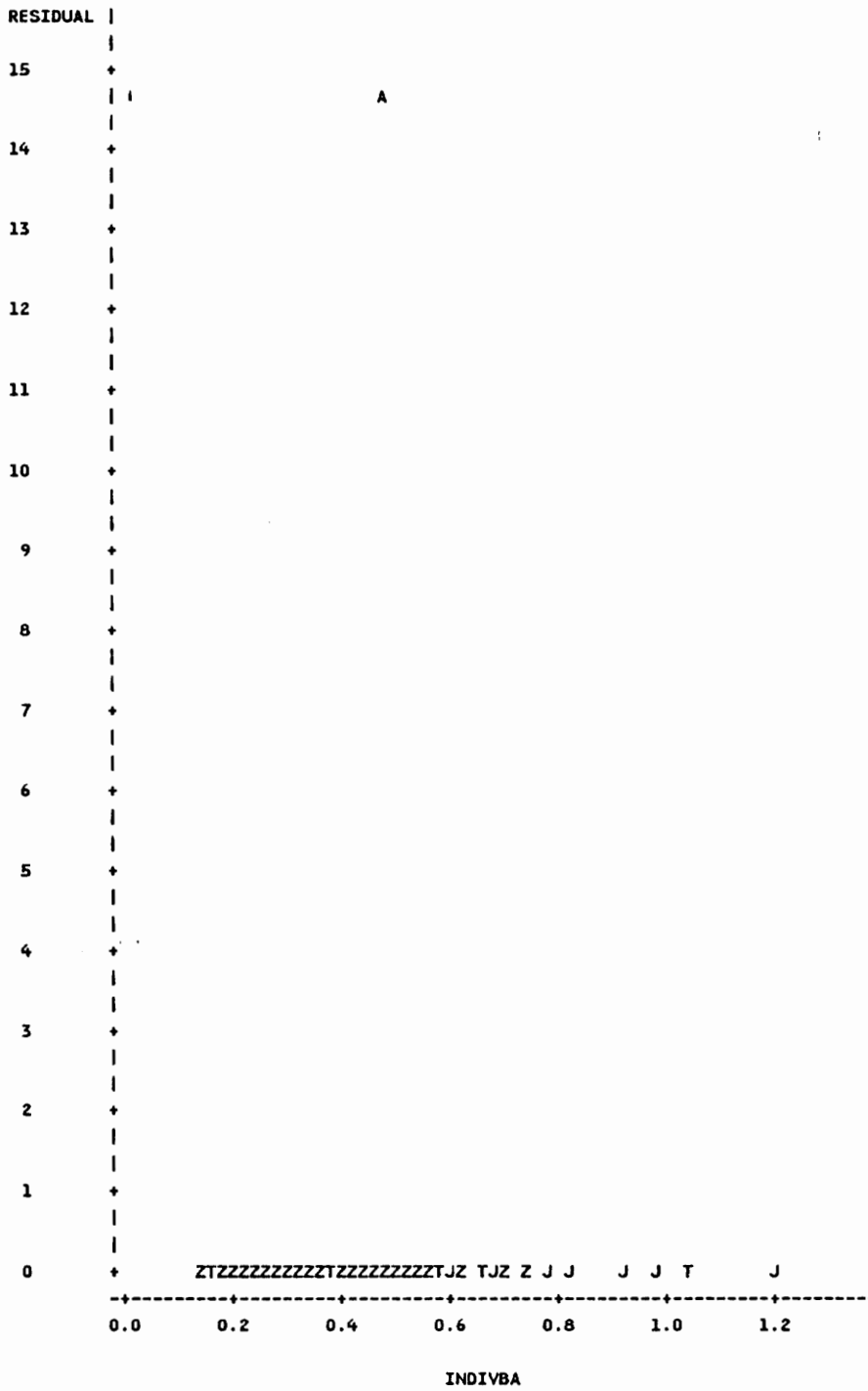


NOTE: 892 OBS HIDDEN

Figure A.17.

STAND=4

PLOT OF RESIDUAL*INDIVBA LEGEND: A = 1 OBS, B = 2 OBS, ETC.

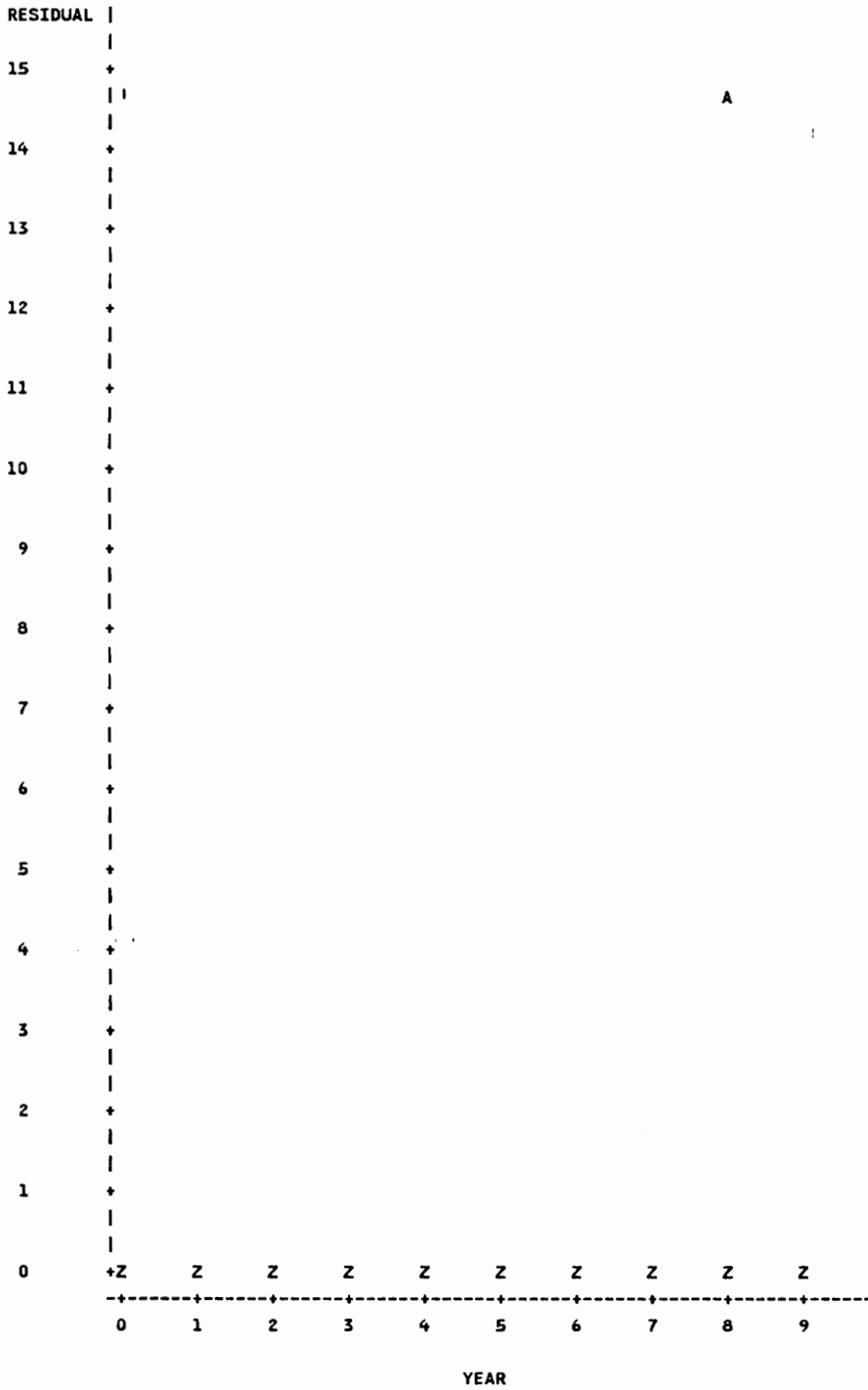


NOTE: 673 OBS HIDDEN

Figure A.18.

STAND=4

PLOT OF RESIDUAL*YEAR LEGEND: A = 1 OBS, B = 2 OBS, ETC.

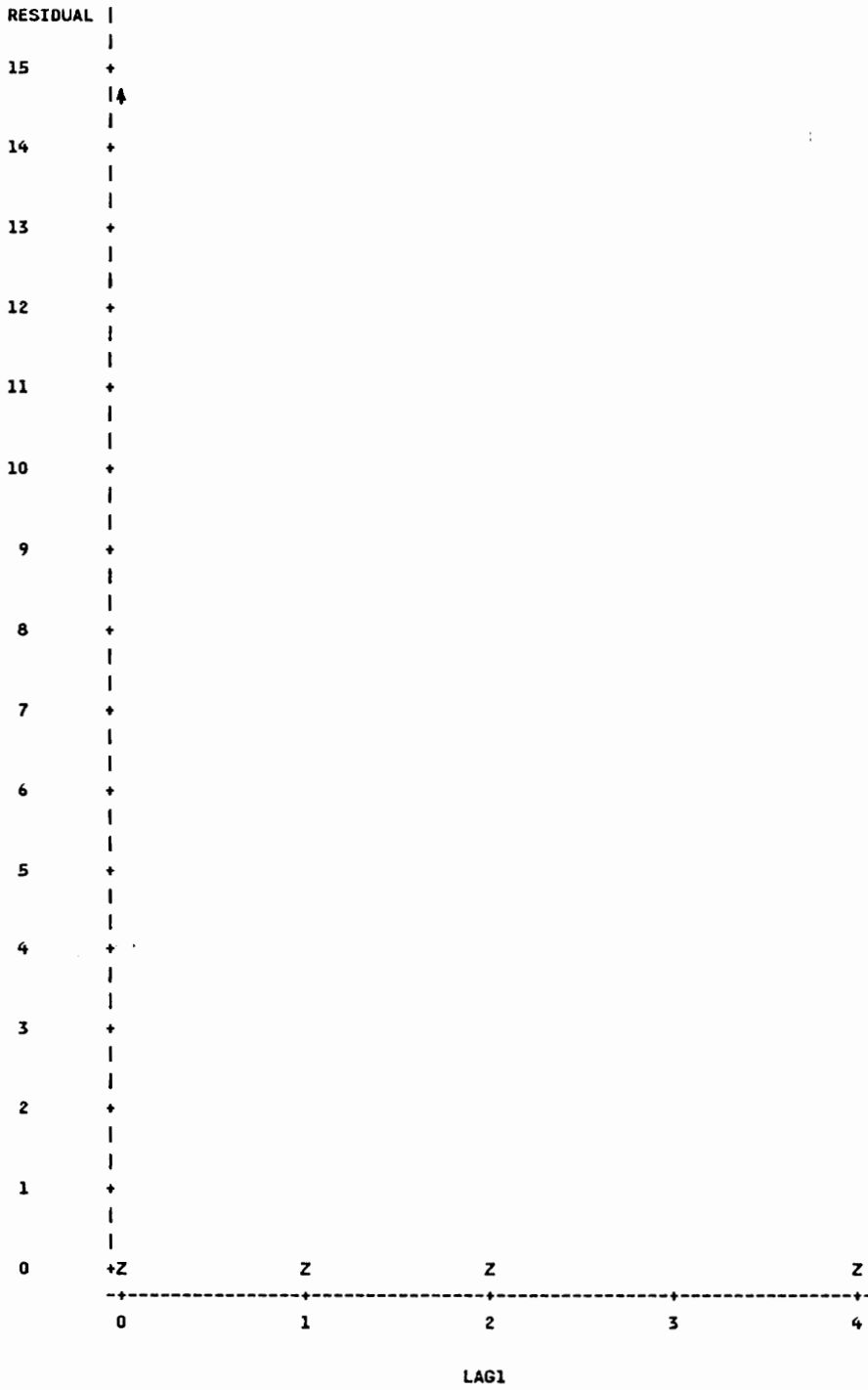


NOTE: 1181 OBS HIDDEN

Figure A.19.

STAND=4

PLOT OF RESIDUAL*LAG1 LEGEND: A = 1 OBS, B = 2 OBS, ETC.



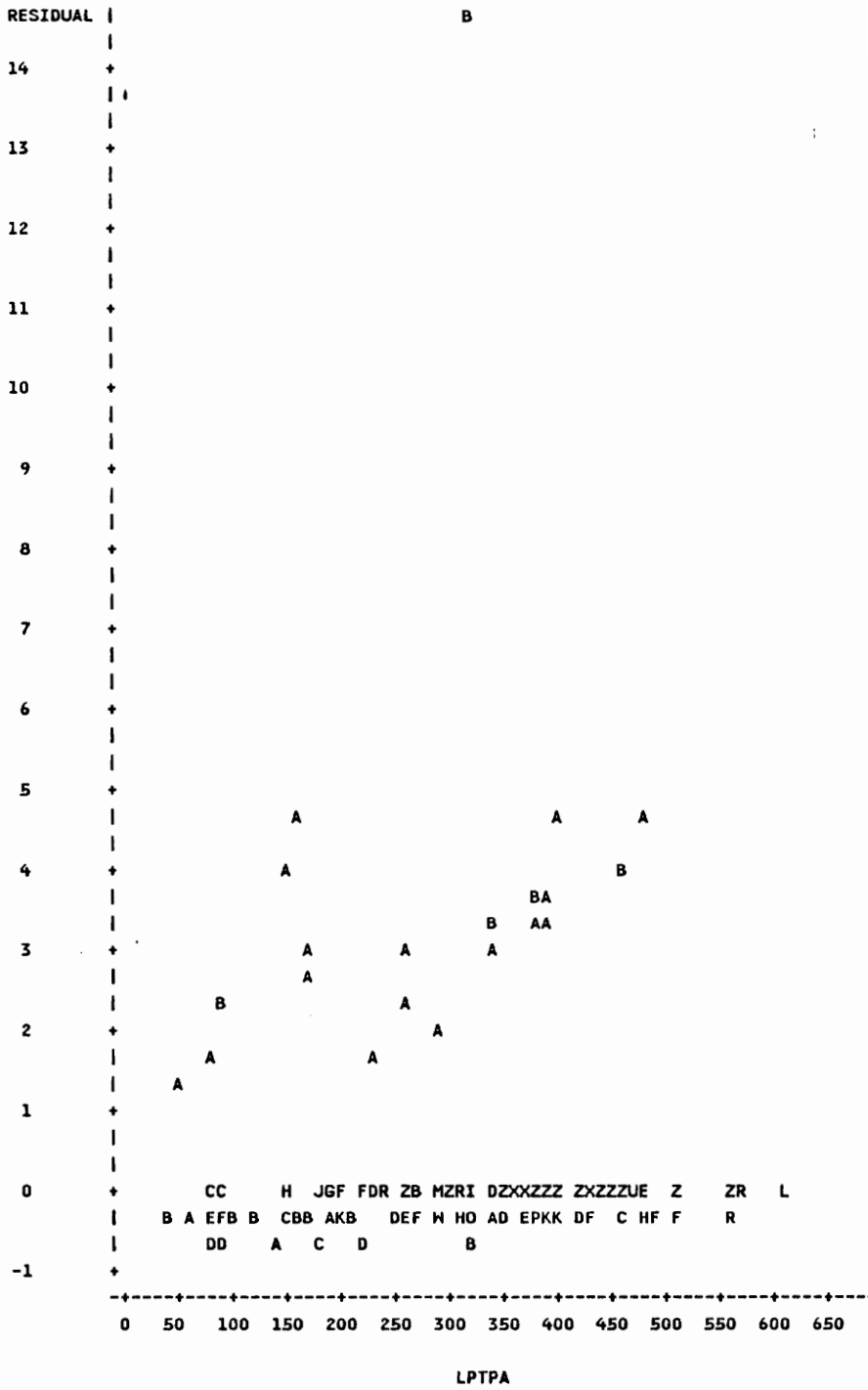
NOTE: 1337 OBS HIDDEN

Figure A.20.

CLASS=5

PLOT OF RESIDUAL*LPTPA

LEGEND: A = 1 OBS, B = 2 OBS, ETC.



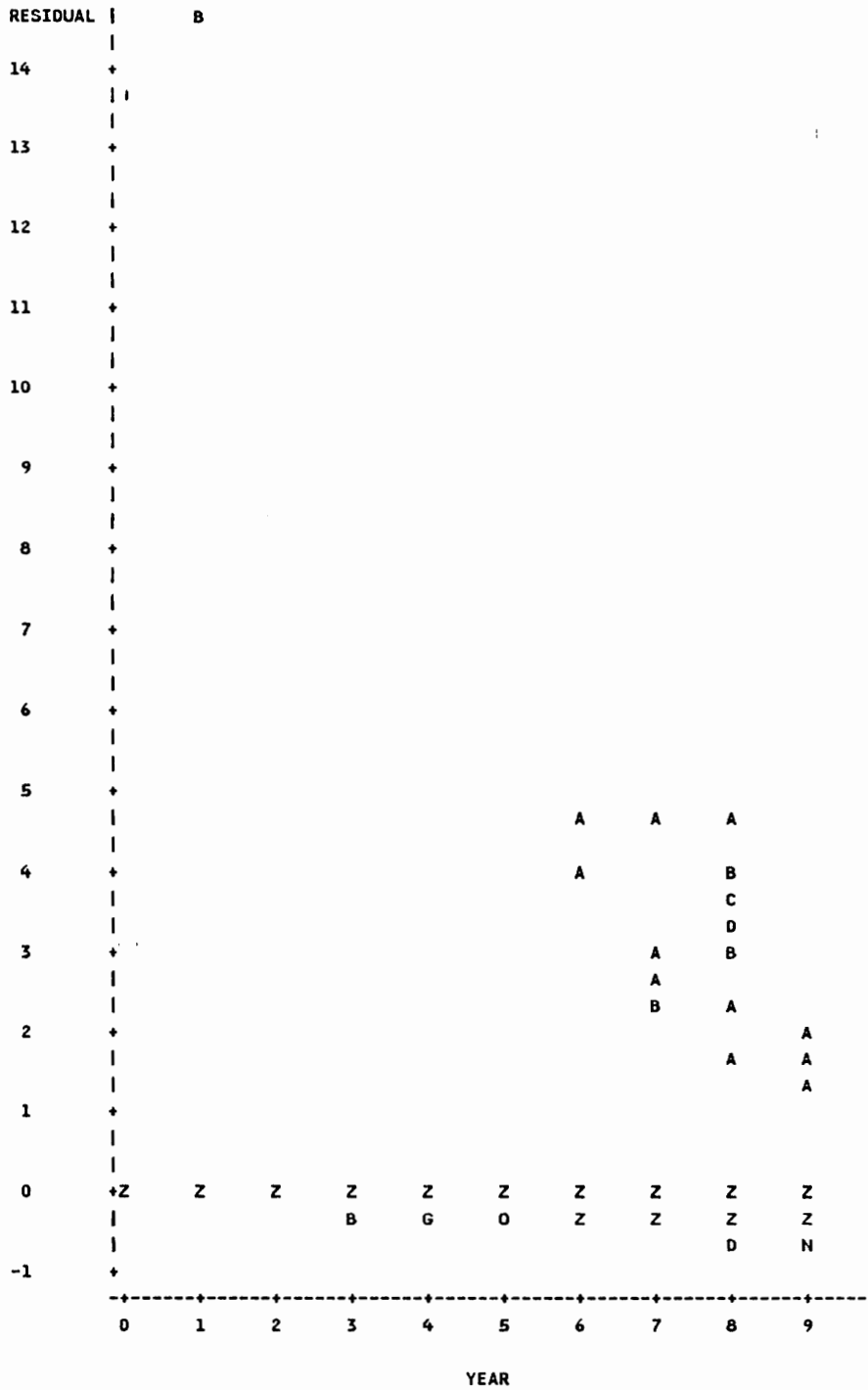
NOTE: 316 OBS HIDDEN

Figure A.21.

CLASS=5

PLOT OF RESIDUAL*YEAR

LEGEND: A = 1 OBS, B = 2 OBS, ETC.

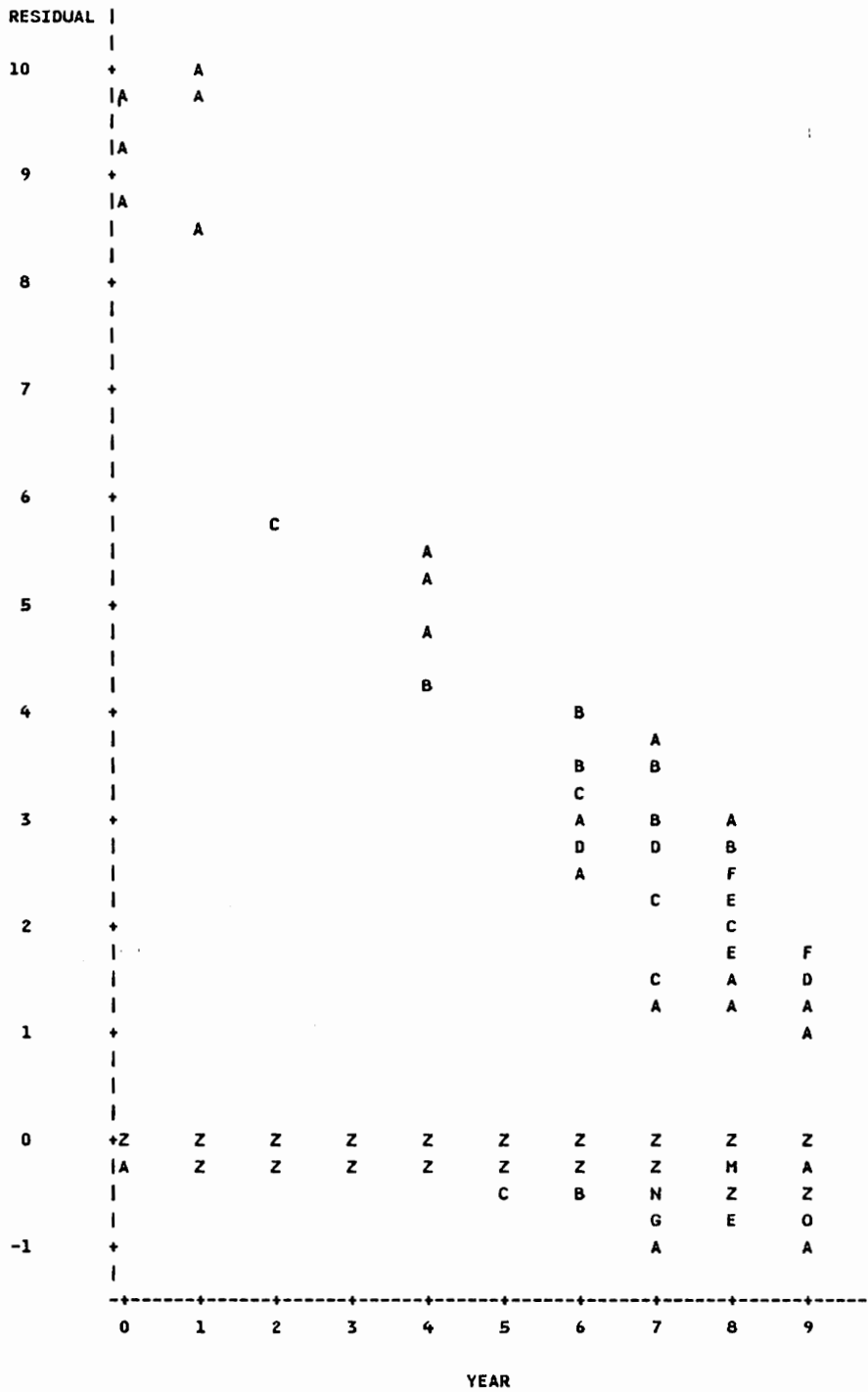


NOTE: 678 OBS HIDDEN

Figure A.23.

CLASS=7

PLOT OF RESIDUAL*YEAR LEGEND: A = 1 OBS, B = 2 OBS, ETC.



NOTE: 1138 OBS HIDDEN

Figure A.26.

CLASS=7

PLOT OF RESIDUAL*LAG1 LEGEND: A = 1 OBS, B = 2 OBS, ETC.

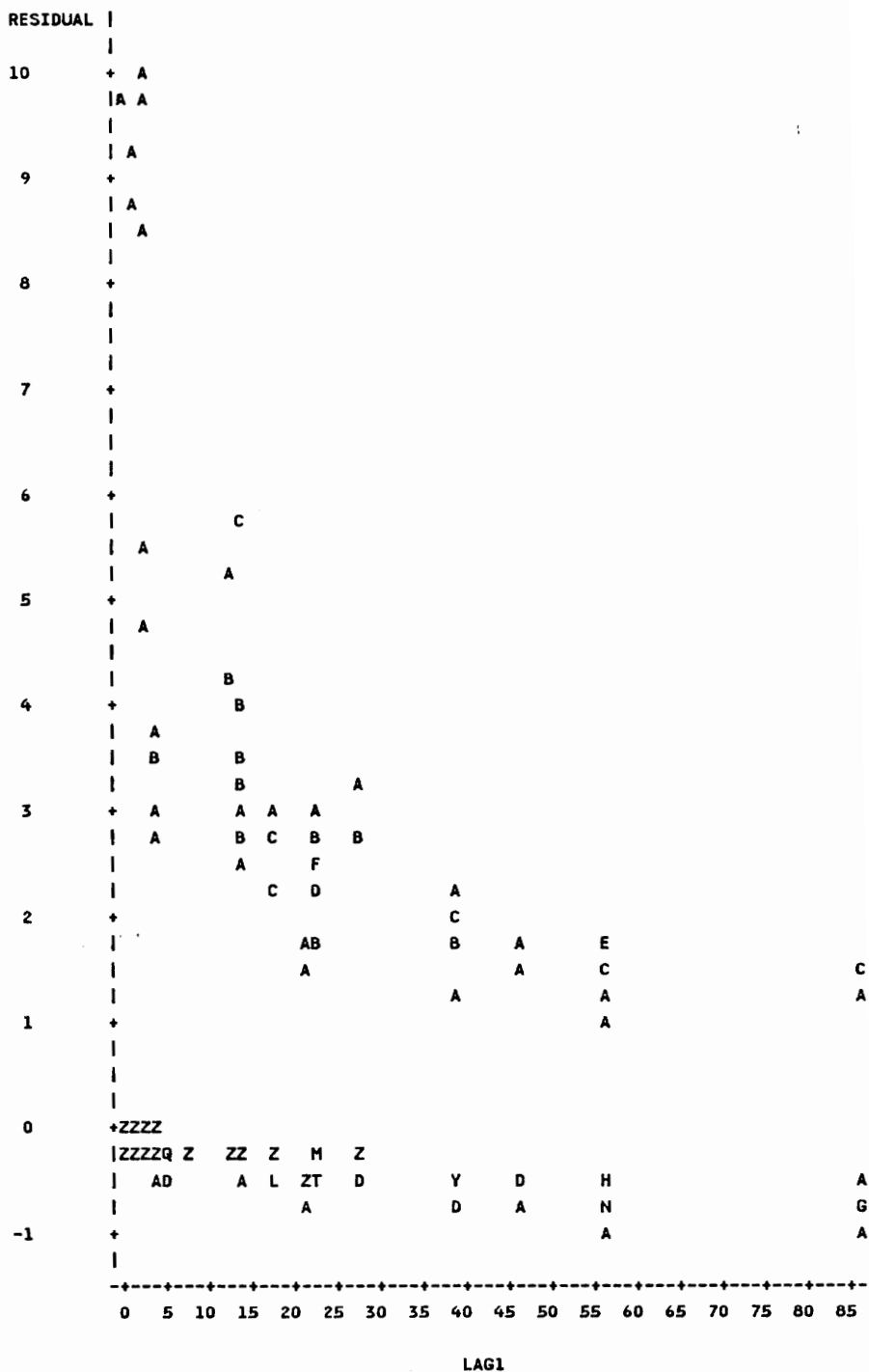
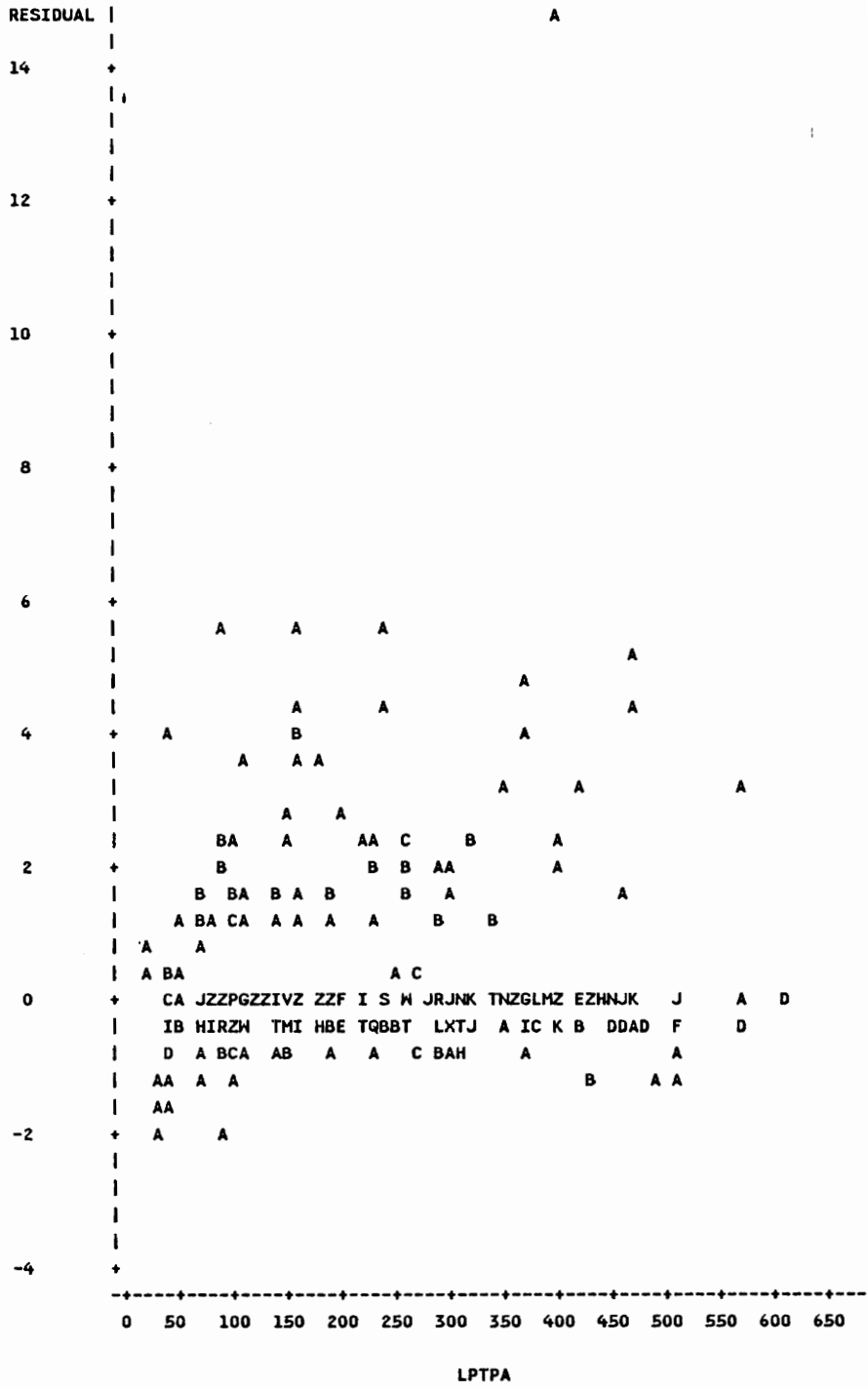


Figure A.28.

CLASS=9

PLOT OF RESIDUAL*LPTPA LEGEND: A = 1 OBS, B = 2 OBS, ETC.



NOTE: 167 OBS HIDDEN

Figure A.29.

CLASS=9

PLOT OF RESIDUAL*INDIVBA LEGEND: A = 1 OBS, B = 2 OBS, ETC.

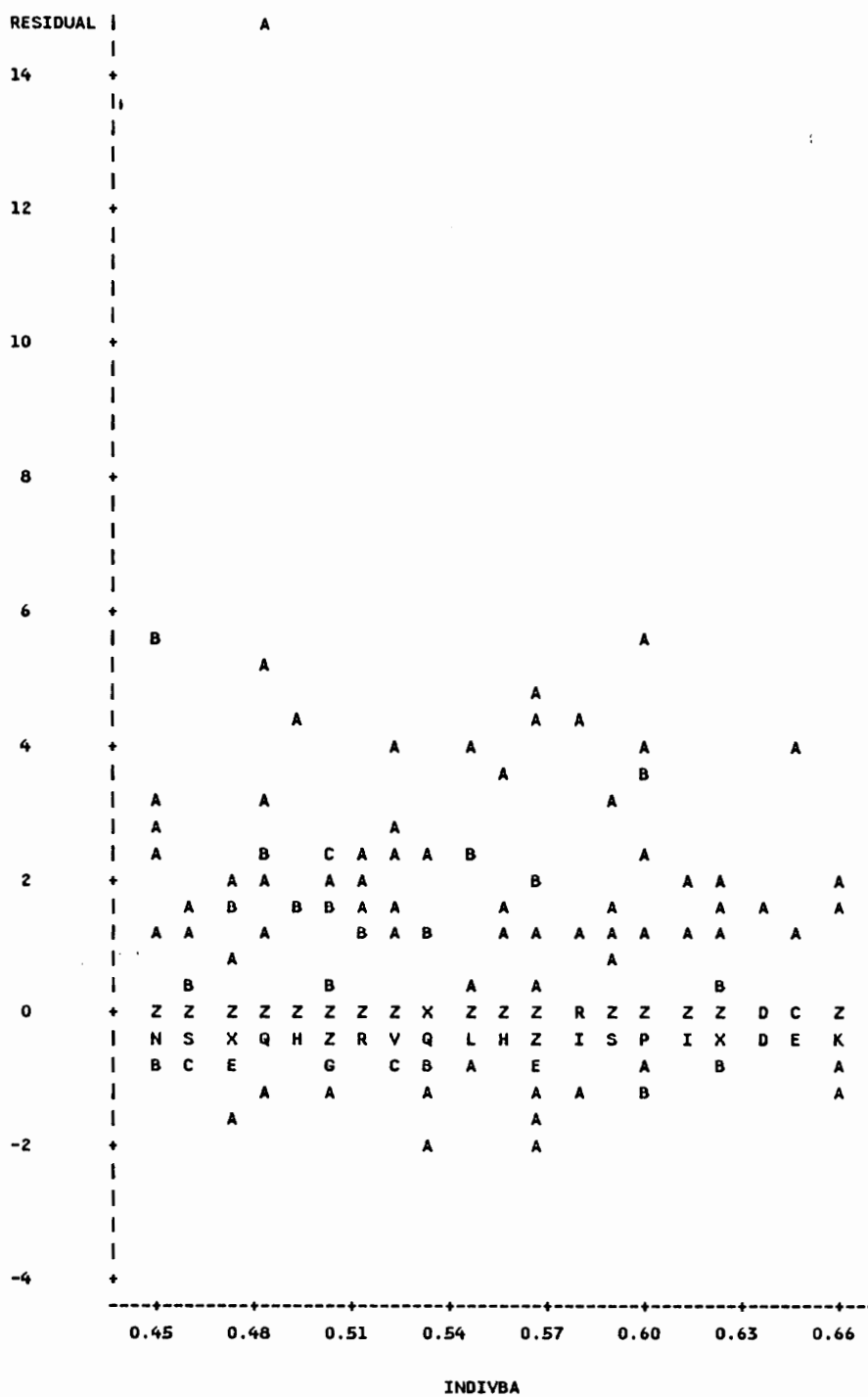
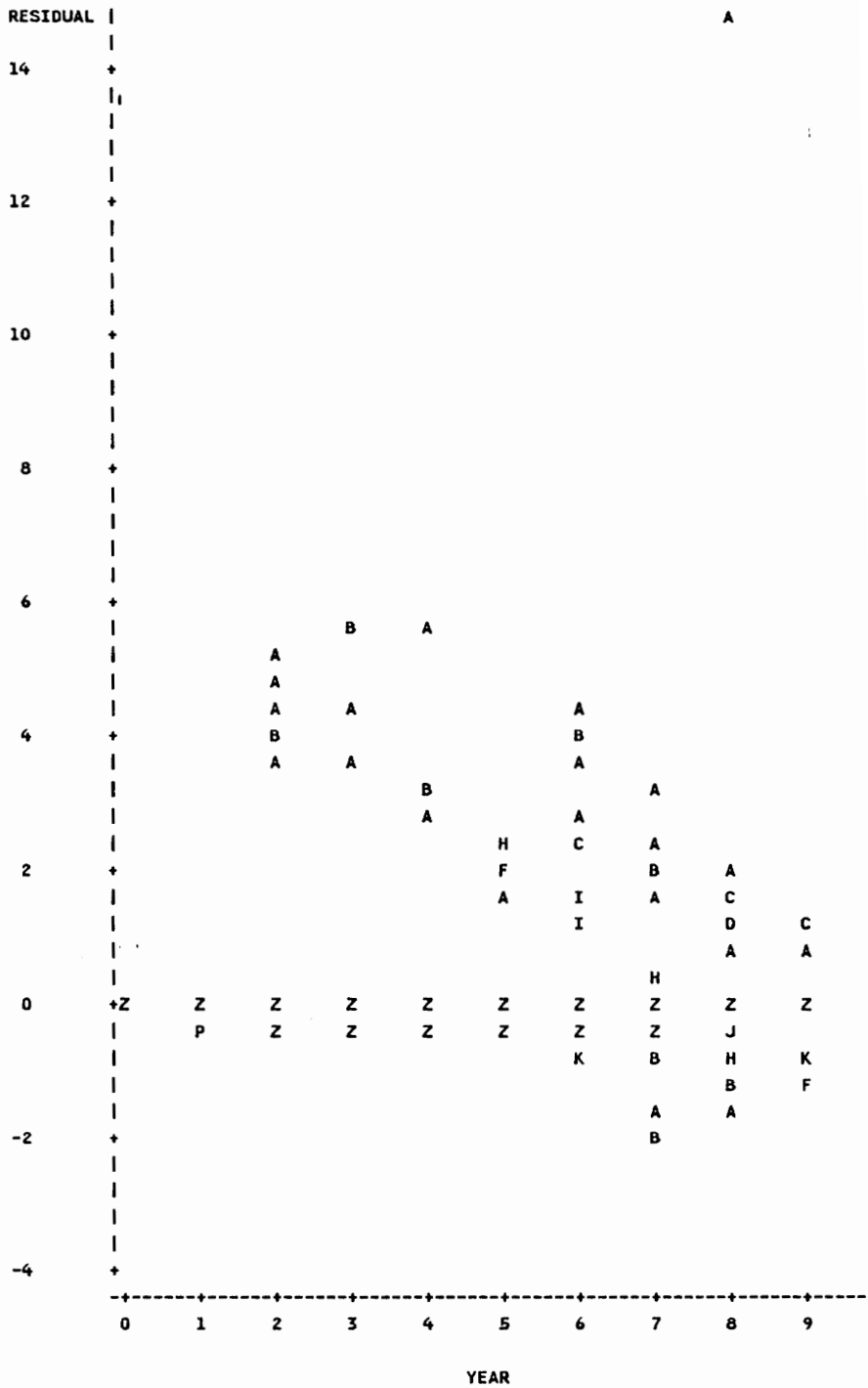


Figure A.30.

CLASS=9

PLOT OF RESIDUAL*YEAR LEGEND: A = 1 OBS, B = 2 OBS, ETC.



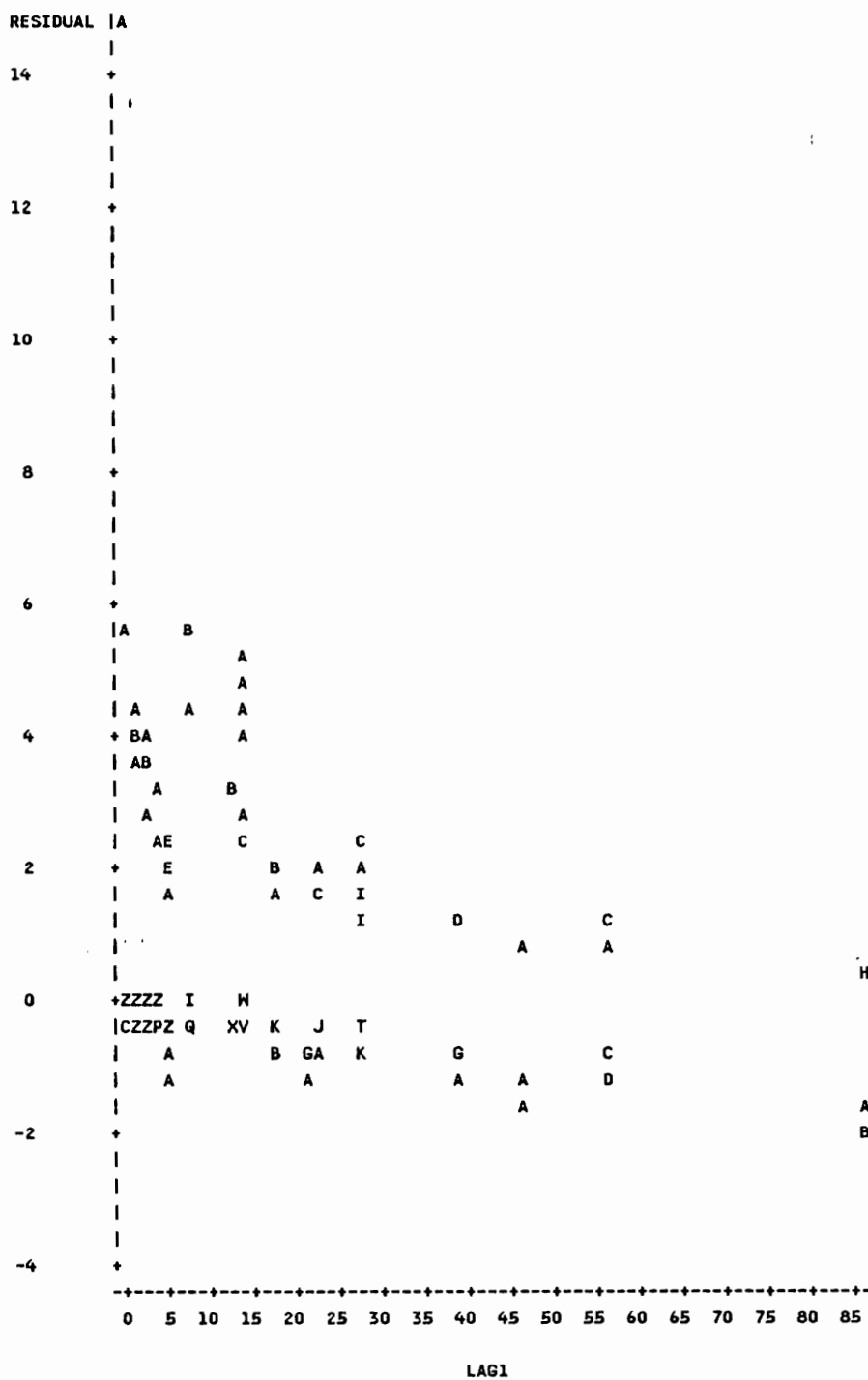
NOTE: 630 OBS HIDDEN

Figure A.31.

CLASS=9

PLOT OF RESIDUAL*LAG1

LEGEND: A = 1 OBS, B = 2 OBS, ETC.

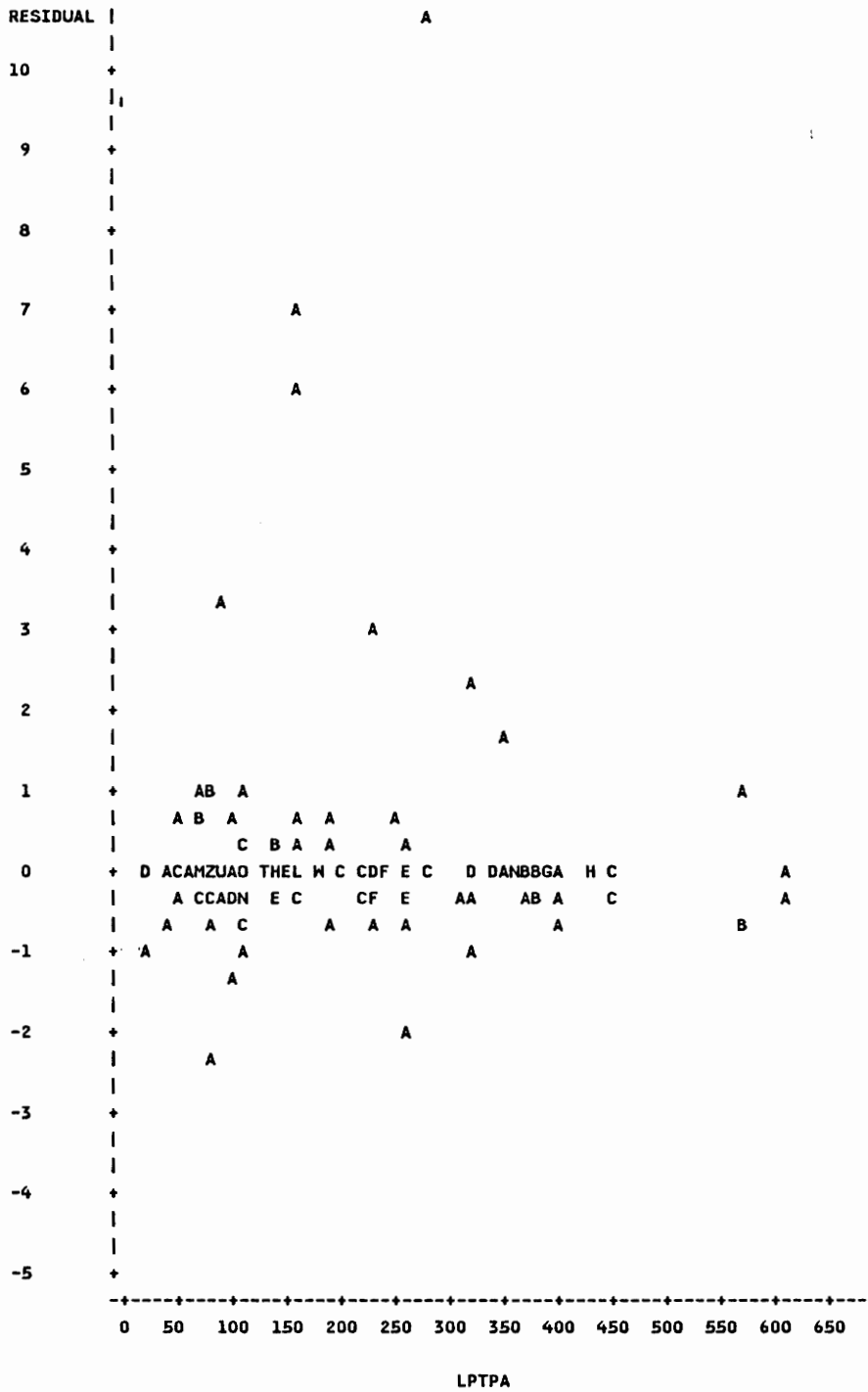


NOTE: 735 OBS HIDDEN

Figure A.32.

CLASS=11

PLOT OF RESIDUAL*LPTPA LEGEND: A = 1 OBS, B = 2 OBS, ETC.



NOTE: 6 OBS HIDDEN

Figure A.33.

CLASS=11

PLOT OF RESIDUAL*INDIVBA LEGEND: A = 1 OBS, B = 2 OBS, ETC.

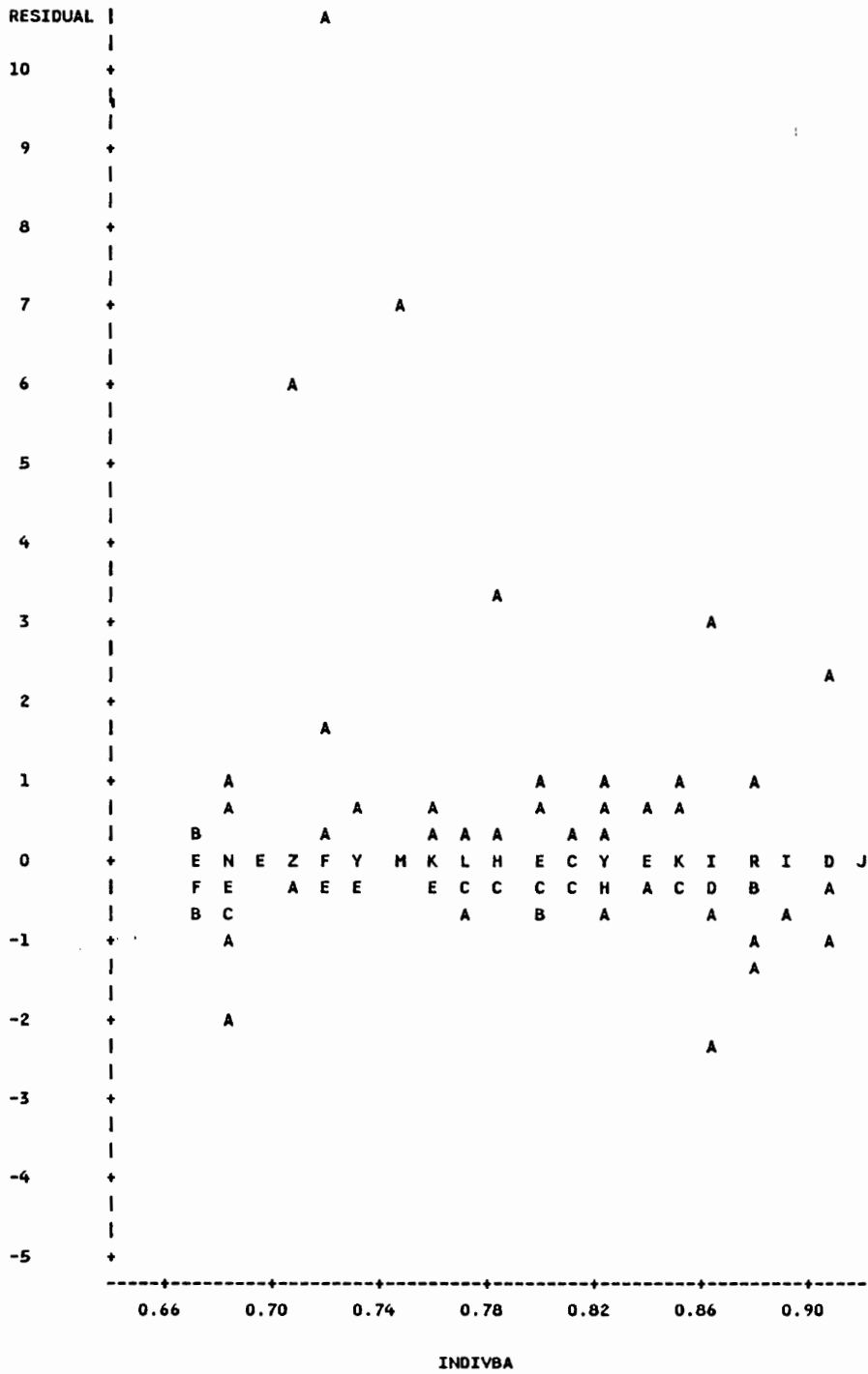
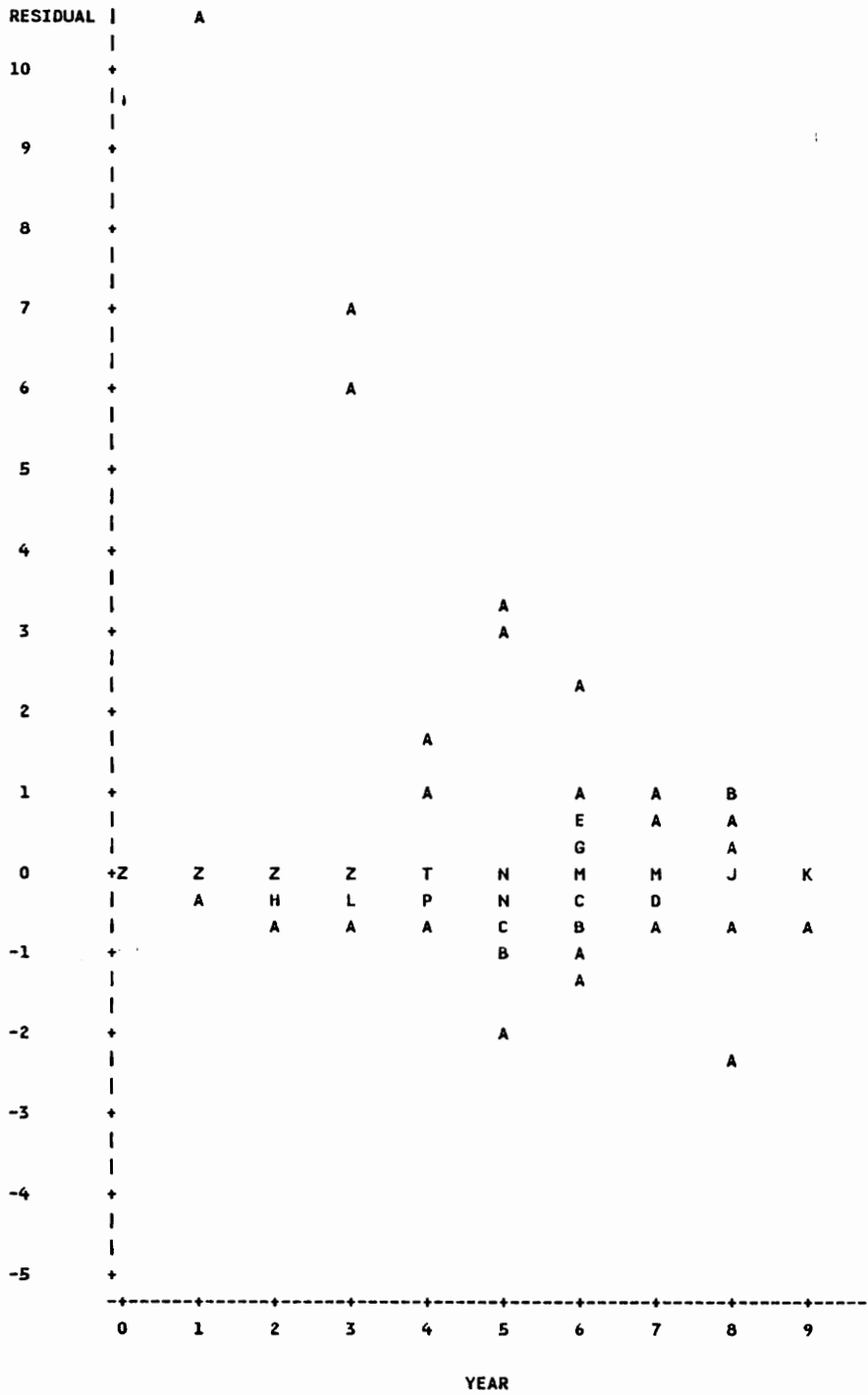


Figure A.34.

CLASS=11

PLOT OF RESIDUAL*YEAR

LEGEND: A = 1 OBS, B = 2 OBS, ETC.

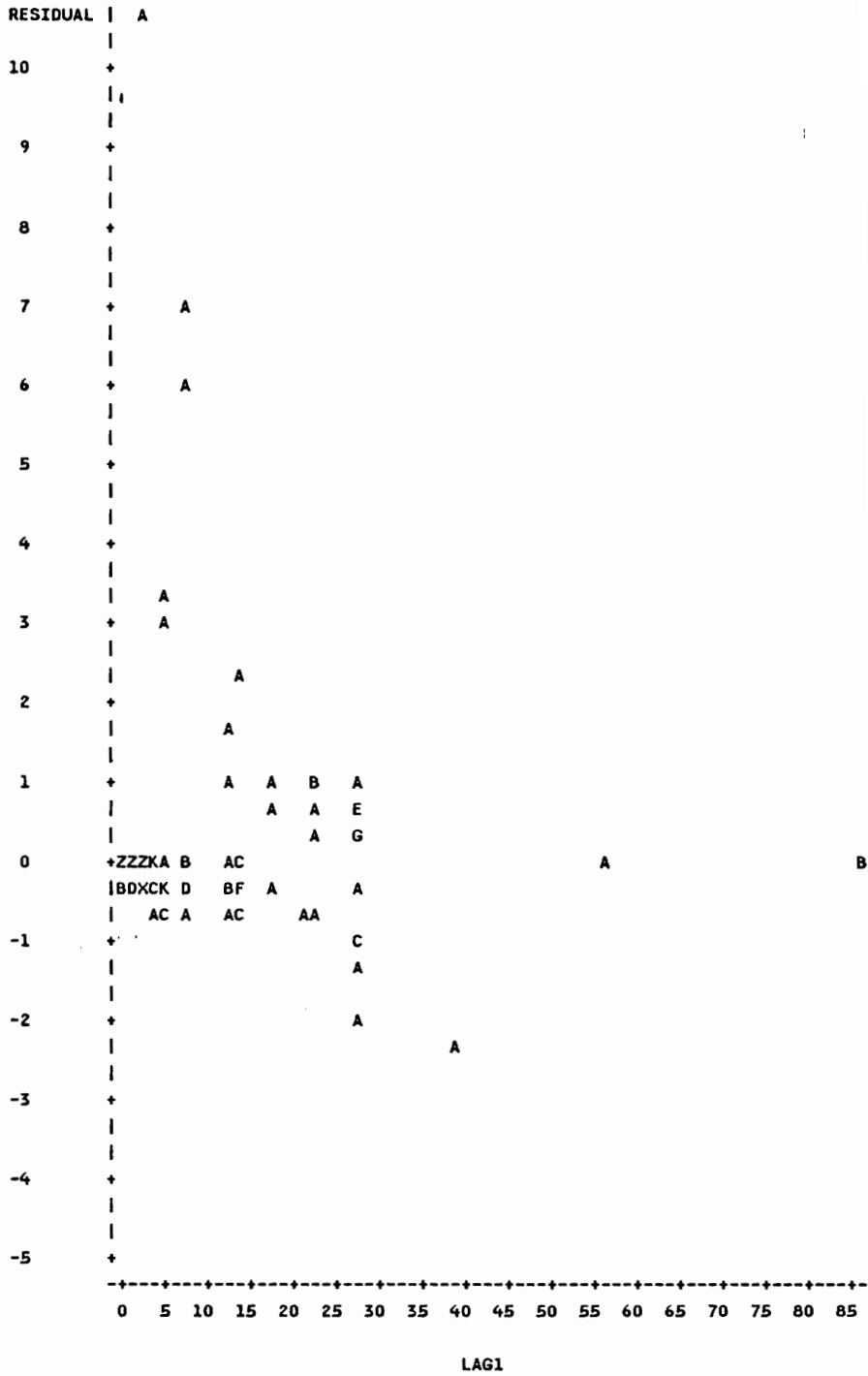


NOTE: 45 OBS HIDDEN

Figure A.35.

CLASS=11

PLOT OF RESIDUAL*LAG1 LEGEND: A = 1 OBS, B = 2 OBS, ETC.



NOTE: 131 OBS HIDDEN

Figure A.36.

CLASS=13

PLOT OF RESIDUAL*LPTPA

LEGEND: A = 1 OBS, B = 2 OBS, ETC.

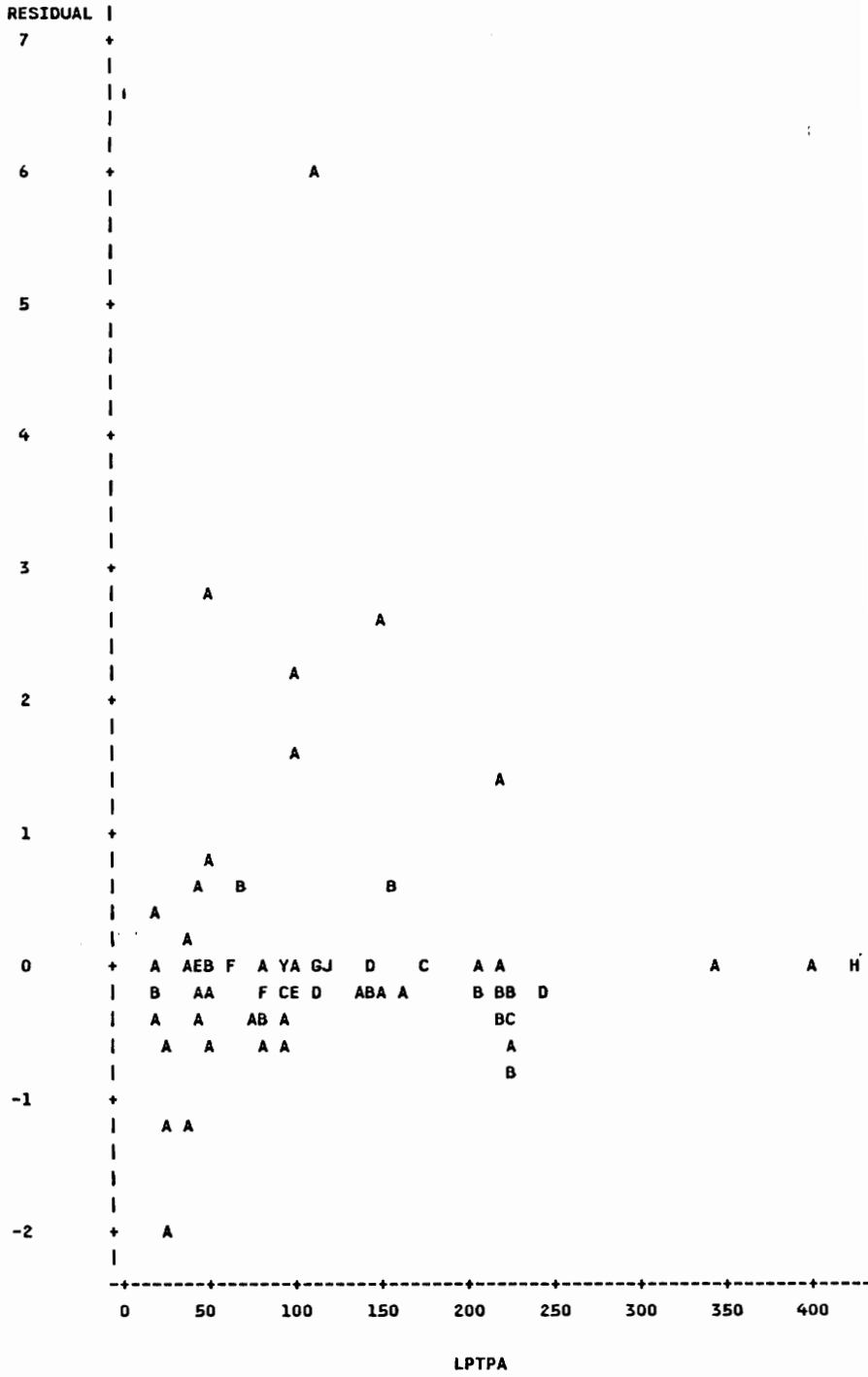


Figure A.37.

CLASS=13

PLOT OF RESIDUAL*INDIVBA LEGEND: A = 1 OBS, B = 2 OBS, ETC.

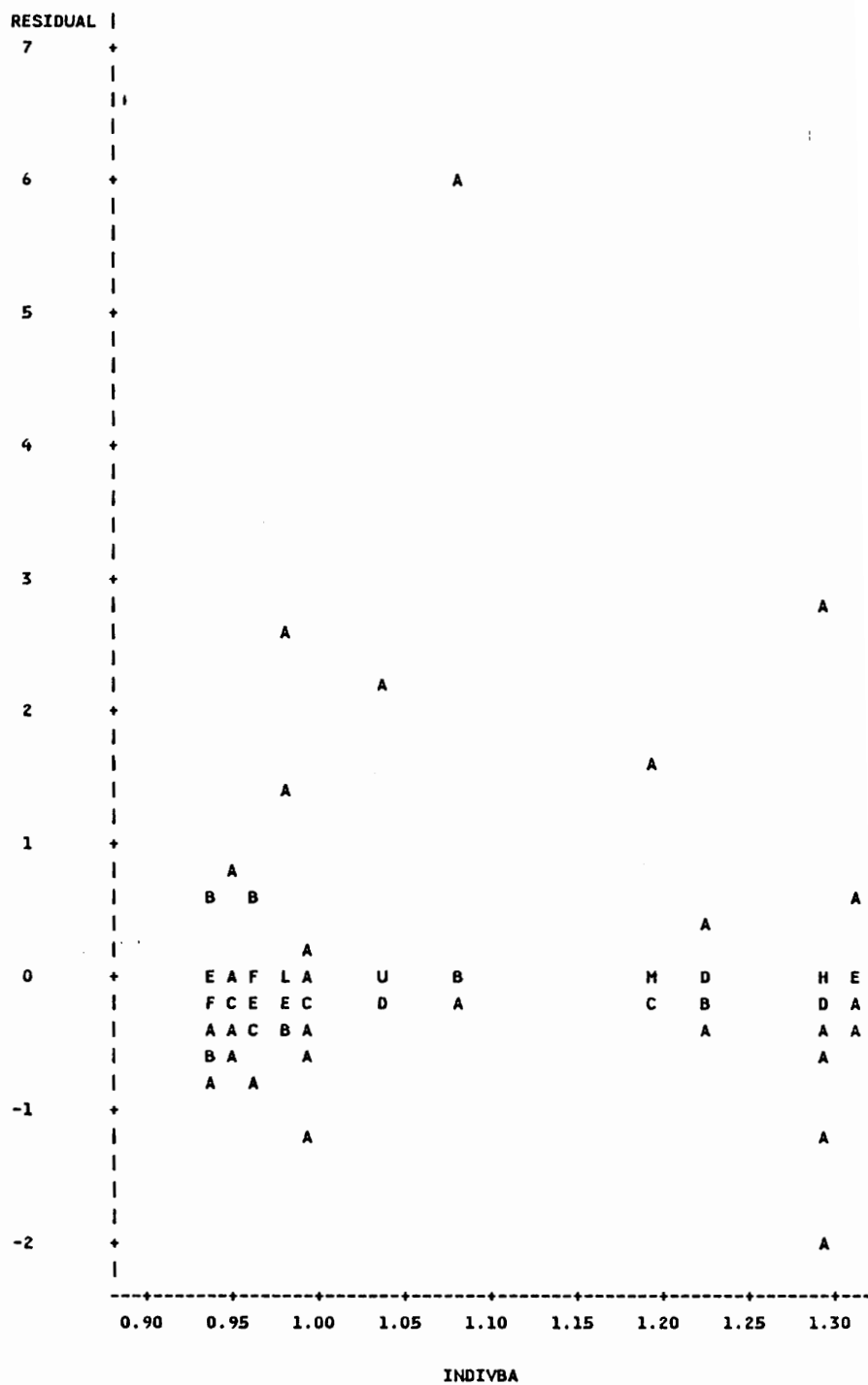


Figure A.38.

CLASS=13

PLOT OF RESIDUAL*YEAR

LEGEND: A = 1 OBS, B = 2 OBS, ETC.

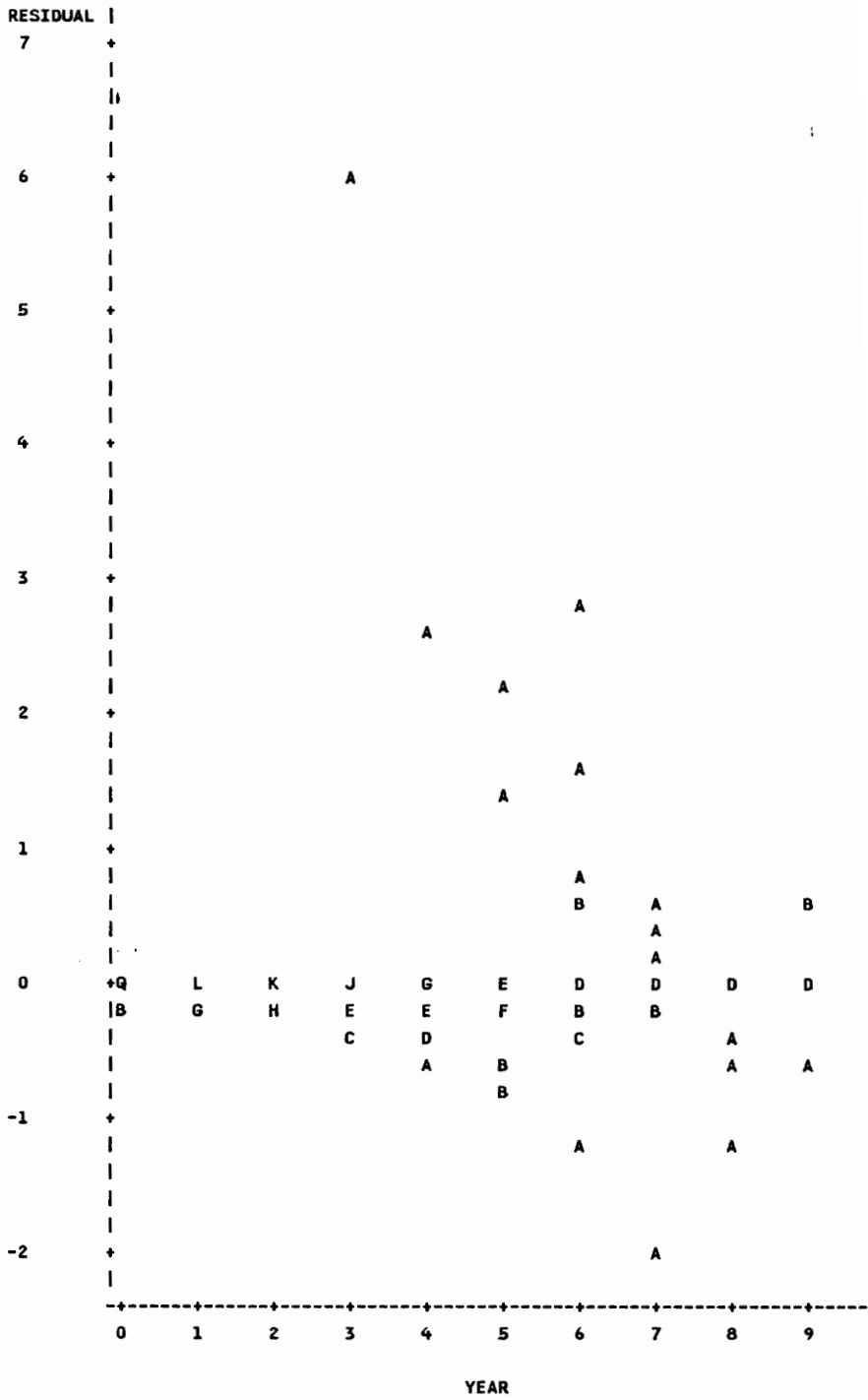
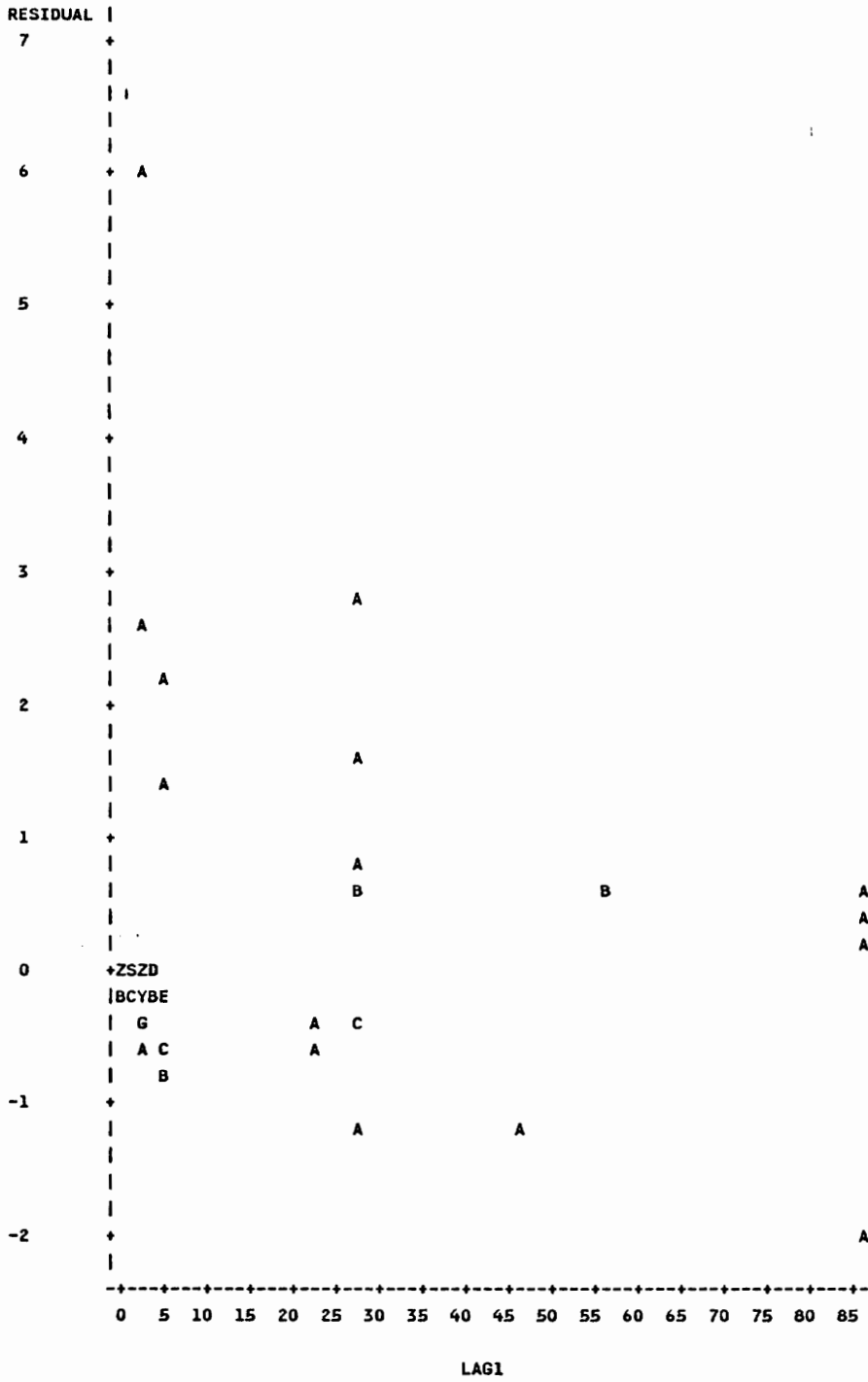


Figure A.39.

CLASS=13

PLOT OF RESIDUAL*LAG1 LEGEND: A = 1 OBS, B = 2 OBS, ETC.

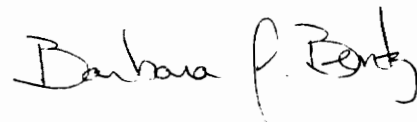


NOTE: 3 OBS HIDDEN

Figure A.40.

Vita

Barbara Joan Bentz was born August 23, 1959 in Fort Worth, Texas. She graduated from Richland Hills High School (in Fort Worth) in 1977. In 1978 she attended Stephen F. Austin State University on a music scholarship, before changing to a forestry major in 1979. After graduating with a B.S. in Forestry and Biology in 1981, she moved to Moscow, Idaho to begin a masters program in forestry. She graduated with a M.S. in Forestry from the University of Idaho in 1983. While in graduate school at the University of Idaho and immediately after graduation, Barbara worked part time for the U.S. Forest Service Mountain Pine Beetle Research Group in Ogden, Utah. After working as a research technician in the Texas A&M Entomology Department, and a 2 year sabbatical in Half Moon Bay, California, she began a doctoral program at Colorado State University in 1987 as a U.S. Forest Service Cooperative Education student. In 1988 Barbara transferred to VPI&SU with her advisor.

A handwritten signature in black ink that reads "Barbara F. Bentz". The signature is written in a cursive style with a large, stylized 'B' at the beginning.