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MATHEMATICAL MODELS.

FOR THE

MOUNTAIN PINE BEETLE-LODGEPOLE PINE

INTERACTION

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Lodgepole pine (<u>Pinus contorta Dougl.</u>) stand and mountain pine beetle (<u>Dendroctonus ponderosae Hopk.</u>) models have been developed, based on 13 years of life and stand sampling (Cole et al. in press). These models incorporate selected years spanning infestations to show interactions.

Conventional modeling procedures, in the absence of finite prior knowledge on the forms of relations, are likely to be insensitive in isolating real, but unique, curve form and interaction information expressed in a data set. Strong, but algebraically undefined, year-d.b.h. interactions were expected; thus we elected to sacrifice statistical evaluation in model development, directly exhausting each data set of the interaction information it contained.

Each model was first developed graphically, utilizing expectation, known constraints, and apparent data trends in arriving at smoothed curve forms. These were carefully fitted through the data by approximate "least deviations." Graphic and descriptor development procedures follow those specified in Matchacurve 1, 2, and 3 (Jensen and Homeyer 1970, 1971; and Jensen 1973).

The base curve used in the stand structure model represents numbers of live trees per acre in each diameter class. Losses to the beetle are extremely small during the endemic period, constituting much less than one tree per acre during any year. Tree mortality during an epidemic can range from less than 1 percent of the 4-inch d.b.h. tree class to more than 85 percent of the 14-inch and greater d.b.h. tree class. Generally, only trees that are larger than 13 inches d.b.h. produce enough beetles to maintain or cause an increase In the infestation rate. This can vary considerably by elevation and latitude.

Curves for beetle life stages show expected survival in a tree of any specific diameter if it becomes infested. Several mortality factors acting on mountain pine beetle populations were evaluated by N. E. Cole (1974); phloem thickness remains the most important factor accounting for differential beetle survival among trees. The rate of phloem drying due primarily to egg gallery construction, and feeding larvae, is probably the next most important factor affecting these populations (Amman 1972).

During Year 8, both emergence and tree losses peak, approximately doubling those of Year 1. Gallery and egg density continue to rise in following years, but emergence declines. About one-half of the trees are killed by Year 8. Loss trends appeared similar for the different diameter classes; but proportionately, losses are much greater for the large diameter classes. In Years 10 to 12, egg

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densities increase to such an extent that high-larval mortality results--probably from severe competition for food, drying of phloem and winter mortality of small larvae. Subsequent emergence, in accordance with expectations, is even lower than in pre-epidemic Years 1 through 5. By Year 12, cumulative tree mortality levels off and annual tree mortality returns to the endemic level. Tree mortality ranges from 49 percent of the 12-inch trees to over 80 percent for trees 19 inches d.b.h. and over.

In these models, the close association of beetle dynamics with numbers and sizes of trees that are infested can be seen at any point in the epidemic. Emergence diminishes rapidly as the large trees are killed. Beetles then tend to infest a higher proportion of smaller trees. Coincidently, gallery starts, gallery inches, and egg densities increase through Year 12, even though emergence declines drastically. Broods in small trees having thin phloem tend toward higher proportions of females than those in large trees having thick phloem. Females survive better under stress (crowding) than males (Cole 1973) and drying of phloem (Amman and Rasmussen 1974).

Starting about the time of peak emergence (Year 8), insufficient males exist to mate females in a relatively short time span. Hence, unmated females continue to produce the aggregative pheromone, which attracts additional females. In the presence of males, the females produce an antiaggregative pheromone, which masks the aggregative pheromone. If, in addition, male mountain pine beetles also produce a powerful antiaggregative pheromone, our theory that increase in attack density over time is related to decrease in proportion of males in the population is supported.

We reason that after most large diameter trees are killed, and the beetle infests primarily small diameter trees (Cole and Amman 1969), the sex ratio shifts further in favor of females. The attack density--and hence gallery inches--then increases. Subsequent larval populations suffer heavy mortality from competition and drying, and emergence declines. The infestation then returns to the endemic level and does not become epidemic again until the stand of lodgepole has grown into diameter and phloem distributions conducive to increased beetle survival and more equal sex ratios.

Ne conclude that beetle dynamics are closely tied to those of lodgepole pine, and that epidemics are strongly dependent upon the presence of large diameter trees having thick phloem.

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