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Dynamics of bark beetle populations: analysis of dispersal and redistribution[1,2]

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The density-dependent bark beetle productivity model proposed by BERRYMAN (1974) is extended to include the effects of survival during dispersal and redistribution on new hosts. The effects of varying food abundance and dispersal, particularly immigration, on the dynamic behavior of the model are evaluated.

The ecology of bark beetle (Scolytidae) populations has been intensively studied over the past half century, particularly in western North America where massive bark beetle outbreaks have occurred since the early 1900's, and in Germany where large outbreaks arose in the years following World War II. Surprisingly there have been few attempts to synthesize this information into a general theory, although THALENHORST (1958) laid a conceptual foundation for such an analysis. The present paper attempts to advance our theoretical understanding of the dynamics of bark beetle populations by incorporating dispersal processes into an earlier model of beetle productivity (BERRYMAN, 1974). Unfortunately, almost all of the research on bark beetle populations has been concerned with changes occurring within infested trees, and there is little empirical evidence on which to base an analysis of dispersal. Hence, much of this paper will be of a deductive nature.

BARK BEETLE PRODUCTIVITY

BERRYMAN (1974) proposed a general model of bark beetle productivity within infested trees. Productivity, or the number of recruits (offspring) produced per parent was expressed as a function of parent density. This function is composed of two counteracting components (fig. 1): First, cooperation between attacking beetles in overcoming the defenses of the host and in pre-conditioning the phloem for larval development (by inoculating fungi and regulating moisture) causes productivity to increase with attack density. On the other hand, productivity declines as attack density increases because of competition for a limited food

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[2] Paper presented at the Conference on «Dispersal of forest insects: evaluation, theory, and management implications», sponsored by the Intern. Union of Forestry Research Organizations (IUFRO), Entomology Dept. of the Swiss Federal Institute of Technology, Zürich and Zuoz, Switzerland, 4-9 September, 1978.

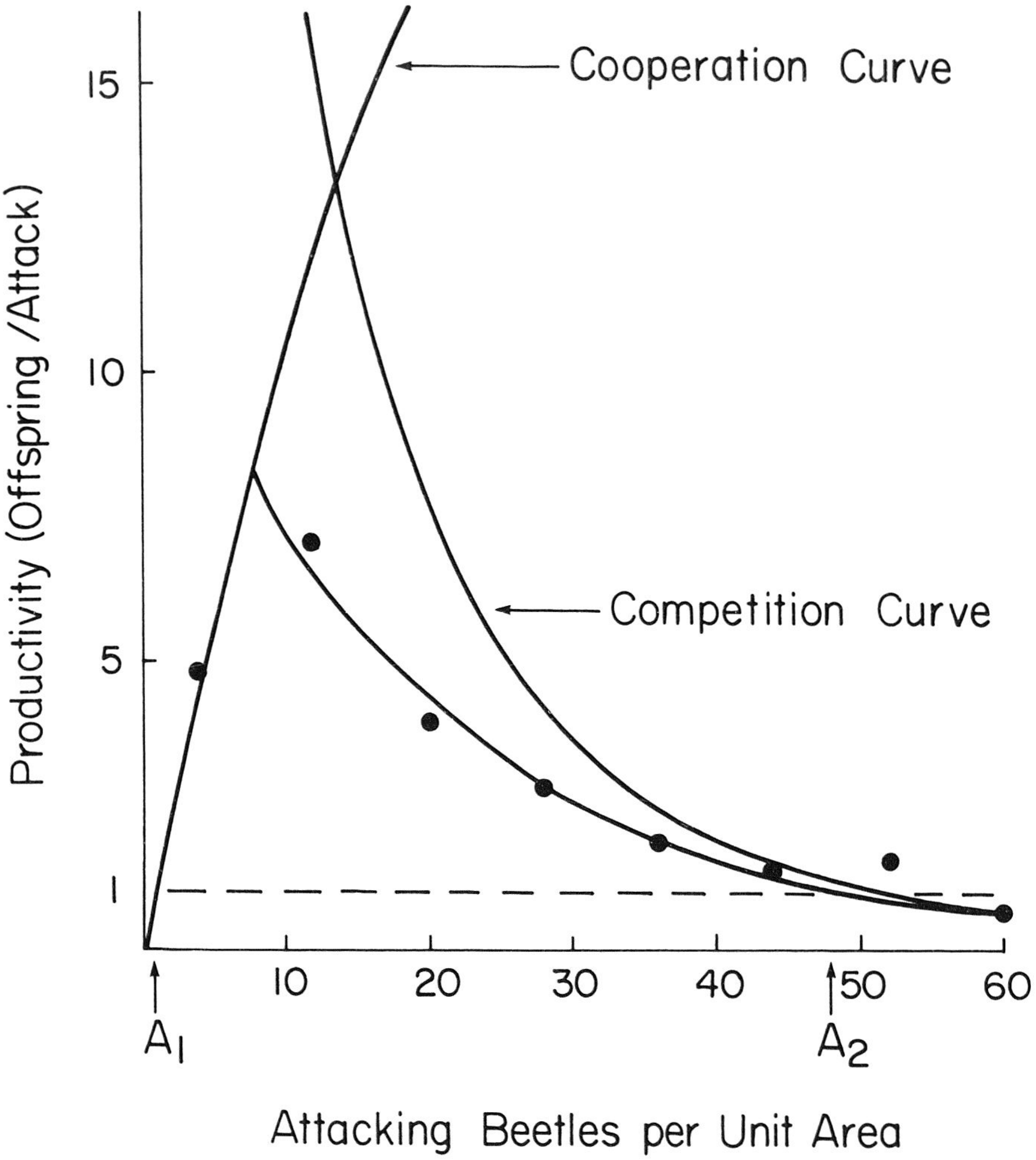

Fig. 1: Productivity curve for the fir engraver beetle, *Scolytus ventralis*, showing cooperation and competition effects and the combined curve fit to field data.

resource and, possibly, greater exposure to predators and parasites. The interaction of these two relationships produces the humpbacked productivity curve shown in fig. 1.

The general equation for this function can be written

$$E/A = f(A) \qquad (1),$$

or

$$E = A\,f(A) \qquad (2),$$

where E is the density of emerging beetles, A is the density of attacking beetles, and f(A) is the density-dependent productivity function. Equation (2) describes the output/input dynamics for individual units of infested host material. However, it is of little help in understanding the inter-generation dynamics of the population. To accomplish this, density in one generation must be expressed in terms of the density in the previous one.

As a start, suppose that all emerging beetles succeed in attacking new hosts and that the quantity of host material remains constant in time. It then follows that

$$A_{g+1} = A_g f(A_g) \quad (3),$$

where A_g is the density of attacks in the gth generation. The function $f(A_g)$ will be identical to equation (1) or fig. 1. It is obvious that when $f(A_g) = 1$ then $A_{g+1} = A_g$ and the system is in equilibrium. From fig. 1 we see that these conditions are met a two points, A_1 and A_2. However, A_1 is an unstable equilibrium because any departure from this point will lead to extinction or growth to A_2, which is a potentially stable equilibrium[3]. Thus, the bark beetle population will inevitably stabilize at, or fluctuate around A_2, or become extinct.

The above analysis is, of course, purely of theoretical interest because the assumptions are rarely true. To develop these ideas further the processes of bark beetle dispersal and colonization must be considered.

DISPERSAL AND REDISTRIBUTION

To understand the processes of dispersal and the resulting redistribution of the population on new hosts we have to expand our view from the unit of host material (e.g., numbers per square meter) to the forest (e.g., numbers per hectare). If we assume a closed system, so that immigration and emigration can be ignored for the present, then the number of beetles attacking per unit area of forest is

$$N_g = A_g H_g$$

and

$$N_{g+1} = E_g H_g$$

where H_g is the quantity of host material infested by the gth generation (e.g., square meters). Inserting in equation (2) produces

$$N_{g+1} / H_g = (N_g/H_g) f(N_g/H_g)$$

or

$$N_{g+1} = N_g f(N_g/H_g) \quad (4).$$

This equation still contains the unreasonable proposition that all emerging beetles survive to attack new hosts. If flight survival could be assumed constant and independent of the emerging population and the quantity of food available, then the problem could be solved by introducing a constant into the right hand side of (4). However, we might well argue that flight survival will increase in direct proportion to the host ratio, H_{g+1}/H_g. A large host ratio would mean that a lot of food is available to a relatively small beetle population and, therefore, their survival should be high. On the other hand, a small host ratio implies little food for a

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[3] One can qualitatively test the equilibrium point by evaluating the behavior of the system following a slight displacement from that point. For example, if the density increases above A_2, productivity will decline below unity and the population will tend to return to A_2. However, stability around the point A_2 depends on the magnitude of the compensatory response, becoming unstable when the return swing causes a displacement to the other side of the equilibrium point which exceeds the initial displacement.

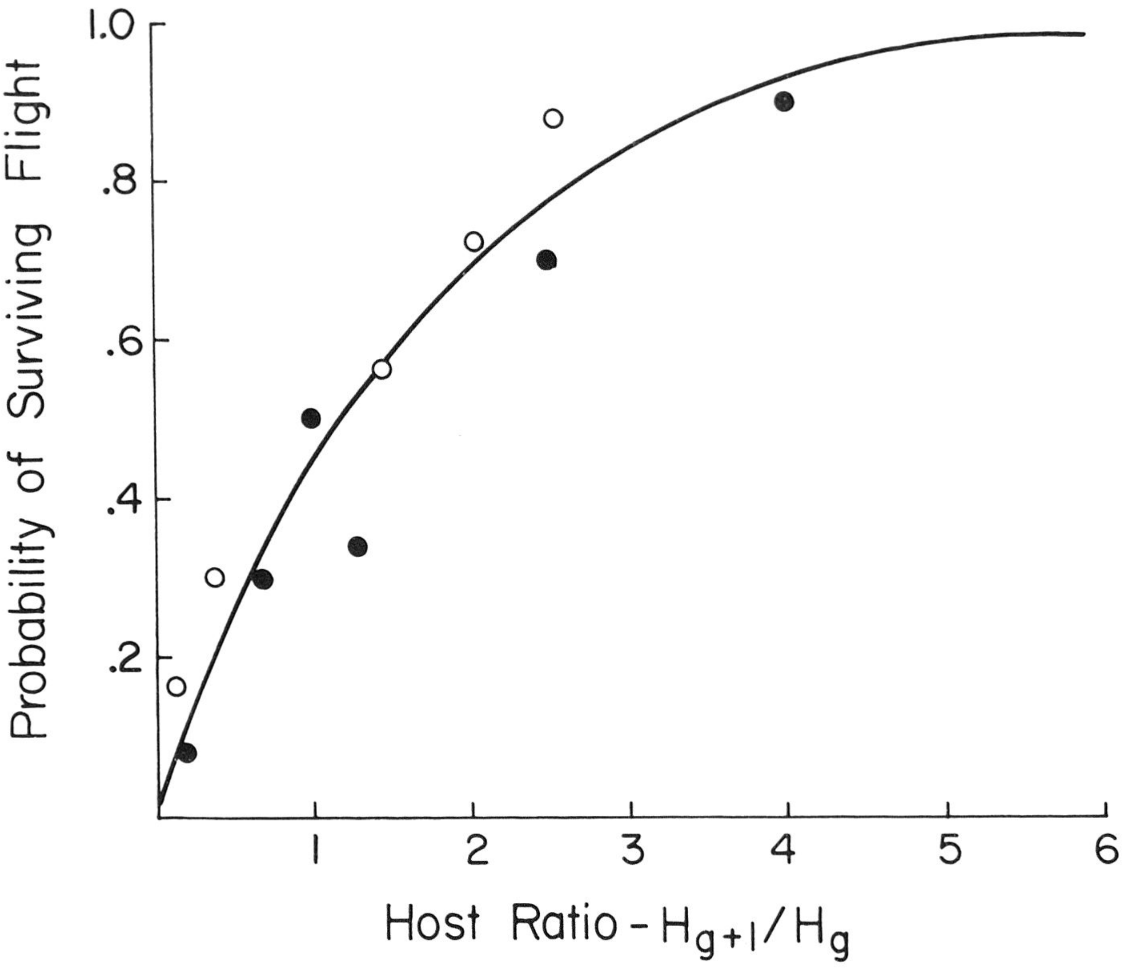

Fig. 2: Observed relationship between the ratio of hosts attacked by one generation to those attacked by the previous one and «apparent survival» (attacking beetles/emerging beetles) during flight and attack (solid points = fir engraver beetle, open points = mountain pine beetle from KLEIN *et al.*, 1978).

large population, and so the chance of a beetle finding and colonizing a host should be small. The empirical evidence that is available indicates that the probability of an emerging beetle surviving to attack a new host is indeed dependent on the host ratio (fig. 2). Inserting the flight survival function into (4) yields

$$N_{g+1} = N_g f(N_g/H_g) h (H_{g+1}/H_g) \qquad (5),$$

For the purpose of analysis let the realized replacement rate or recruitment rate (i. e., attacking offspring/attacking parent) of the population be

$$R = f (N_g/H_g) h (H_{g+1}/H_g) \qquad (6).$$

Obviously, when $R > 1$ the population is growing, when $R < 1$ is declining, and $R = 1$ it is in equilibrium. From (6) we see that the replacement rate is determined by the density-dependent productivity function (fig. 1) and the redistribution function (fig. 2). The population will grow if either the relative density of attacks per unit area of host material is low or the host ratio is high, and will decline in the opposite situation.

Many bark beetle populations exist for long periods of time at very low levels. At such times they are said to exhibit «endemic» behavior. Under certain conditions, however, population explosions, outbreaks or «epidemics» erupt which only subside after large numbers of trees have been killed. Let us attempt to interpret this dynamic scenario using equation (6).

Suppose a large forest system exists in which the food supply for bark beetles is scarce and remains relatively constant for a long period of time; i. e., the host ratio approximates unity and the function h is constant. A bark beetle population in such a system will grow until N_g/H_g, the attack density, equilibrates at a replacement of one, according to the replacement function (6). This is the «endemic» pattern of behavior. Now suppose that, as a result of some environmental disturbance such as windthrow, defoliation or drought, a large quantity of food suddenly becomes available (i. e., $H_{g+1} >> H_g$). Recruitement, R, will increase because of the large host ratio and low attack densities and an epidemic will erupt. The population will grow as long as $H_{g+1} > H_g$ but will decline as the food supply is exhausted. Thus, equation (6) appears to adequately describe the observed behavior of some bark beetle populations.

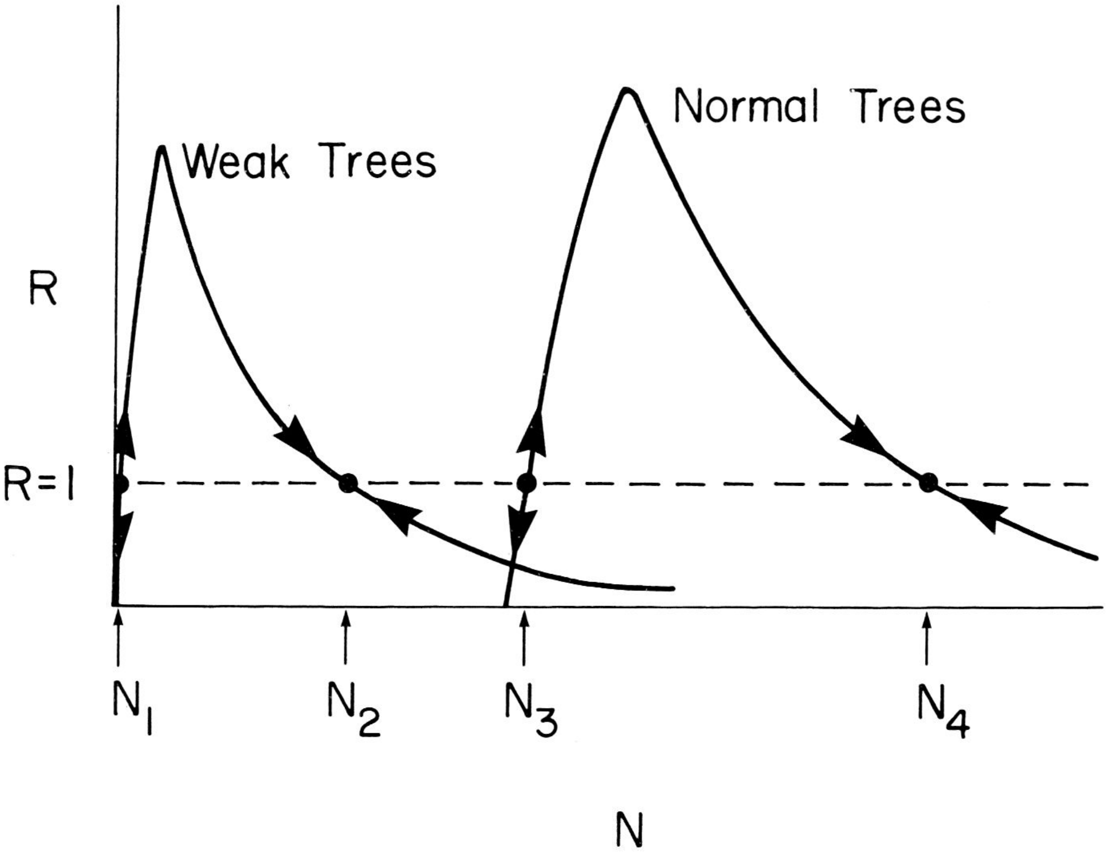

Fig. 3: Replacement curves for endemic and epidemic beetle populations, where reproduction in the normal healthy trees is only possible when beetles attain sufficient numbers.

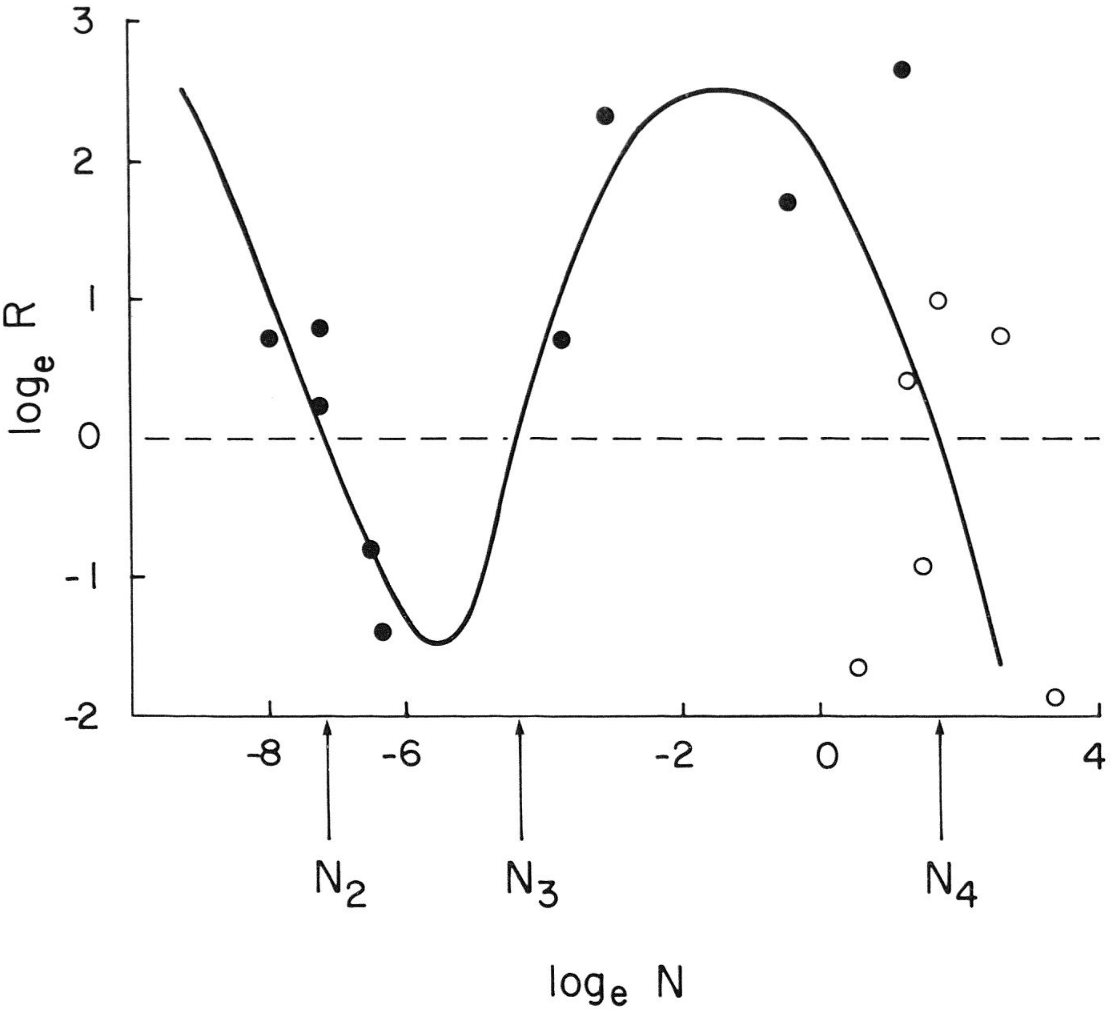

Fig. 4: Replacement curve for the mountain pine beetle, *Dendroctonus ponderosae,* constructed from data in TUNNOCK (1970) and survey reports for the Glacier National Park epidemic (solid points) and from PARKER (1973) (open points); note the endemic equilibrium N_2 at 0.0008 trees per acre per year, the epidemic threshold, N_3 at 0.012 trees per acre, and the epidemic equilibrium, N_4 (which, of course, is not maintained) at 5.47 trees per acre per year. $R = N_{g+1}/N_g$, where N_g is the number of trees killed per acre in year g.

The interpretation of bark beetle epidemiology becomes even more intriguing when we consider the concept of «primary attack» (THALENHORST 1958) or «critical beetle population level» (BERRYMAN, 1978a). These, and other authors, suggest that small beetle populations are incapable of successfully invading healthy trees because they cannot aggregate sufficient numbers of beetles in a short enough time span to overcome the defense systems of these trees. However, once populations have built up to a critical level, say in windthrows, then primary attack may be possible and an epidemic erupts. BERRYMAN (1978a) emphasized that this critical beetle population must be related to the overall health, or vigor, of the stand.

In terms of equation (6) we are implying that the food supply is independent of beetle population size as long as the critical population level is not exceeded.

Above this level, however, the food supply increases substantially. This idea can be expressed mathematically as follows

$$R = f(N_g/H_g)\, h(H_{g+1}/H_g) \qquad (7a),$$

$$H_g = k(V),\ N_g < N_c \qquad (7b),$$

$$N_c = m(S) \qquad (7c),$$

$$H_g = p(N_g)\,(T - H_{g-1}),\ N_g \geqq N_c \qquad (7d),$$

where k(V) expresses host availavility as a function of external environmental variables (e. g., lightning strikes, windthrows), N_c is the critical beetle population level expressed as a function, m(S), of the health or vigor of the stand, $p(N_g)$ is the proportion of the available hosts actually infested, and T is the total available host material from which is subtracted the quantity infested by the previous generation of beetles.

In effect two replacement curves now exist, one for the «endemic» population obeying equations (7a) and (7b) and one for the «epidemic» population obeying (7a) and (7d). The combination of these two curves produces a replacement function with 4 potential equilibrium points (fig. 3); a detailed discussion of the properties of such curves can be found in TAKAHASHI (1964) and BERRYMAN (1978 b). Two of these equilibrium points are unstable: N_1 the extinction threshold and N_3 the critical beetle population or «primary attack» threshold, and two are potentially stable, N_2 the «endemic» equilibrium and N_4 the «epidemic» equilibrium. Of course, equilibrium at N_4 is unlikely to occur because the host ratio changes continuously during the «epidemic» cycle. That some bark beetle populations may indeed be governed by double-humped replacement curves is illustrated in fig. 4.

From fig. 3 we can visualize how bark beetle outbreaks may be initiated. Given a population at its «endemic» level, N_2, then it may attain its critical threshold, N_3, if (1) the quantity of weakened host material increases raising the equilibrium point above N_3, (2) the vigor of the normal trees in the stand declines lowering N_3 to the endemic population level N_2, or (3) beetle immigration from surrounding areas raises the attacking population above N_3. This last conclusion is extremely important because it implies that, even if the conditions required to initiate an outbreak are only present in a restricted locality, the outbreak may spread over vast forested areas. For instance, a small group of trees may become stressed by root diseases, fire, etc., allowing beetle populations to increase locally. In the next generation these beetles may invade adjacent stands raising the local populations above their critical population levels, and so on. Hence, the model helps explain the devastating outbreaks of the mountain pine beetle which have spread like wildfire through apparently health lodgepole pine stands in western North America.

The dispersal influence also poses other severe management problems. Political or ownership boundaries are not respected by dispersing bark beetles. Hence, one owner may be practicing sound forestry, by growing healthy stands free of bark beetles, only to be destroyed by immigrants from his neighbors' lands.

In conclusion, the well-developed dispersal and host colonization abilities of bark beetles make them difficult pests to manage without a coordinated, areawide, effort to maintain stand vigor, and to locate and deal with outbreak epicenters.

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