Populations of many insect species are regulated at sparse densities for long periods of time by the action of natural biological control processes. This is particularly noticeable in relatively undisturbed ecosystems, such as forests, but may also occur in highly artificial agro-ecosystems. Under these conditions, the insects are rarely considered pests because they do not normally exceed economic damage levels. However, on occasion, some of these populations may escape the influence of their controlling factors and erupt to high densities, wreaking destruction on humans, their crops, or forests (Fig. 1). Although these characteristics of pest outbreaks, or epidemics, have been recognized for many years, no general and practical framework has been presented for evaluating and predicting insect outbreaks. In the present paper I propose an elementary yet general model for describing eruptive insect population dynamics, and show how it can be applied to estimating outbreak probabilities.

Biological Control

For the purpose of this discussion, we will consider biological control to be the regulation of a population by any natural biological process. Thus, in addition to the usual examples of biological control of pests populations by parasites or predators (i.e., "control from above"), we also include the regulation of populations at low densities by host resistance or any other property of their food (i.e., "control from below") (Fig. 2). For example, moth and beetle populations (Coleoptera: Scarabaeidae) are prevented from reaching their potential abundance because of high resistance to attack in the majority of the trees in the forest (Berrymon 1979a, 1979b). From this point of view, then, biological control is a result of trophic interactions between two or more species which maintain one or more of the populations at densities considerably lower than their potential. Support for this view can be found in classical examples of biological control of introduced weeds and insect pests (see Clausen 1958, and Hoffaker 1959).

Control Efficacy and Tolerance

Biological control processes are able to control pest populations because their negative impact on the population increases with pest population density. In other words, they function as negative feedback regulators of pest population density by imposing lower survival or reproductive rates on the population as it increases (Fig. 3). If the control process operates effectively at all population densities (Fig. 3a), then regulation will be maintained at all pest densities and outbreaks will never occur. However, some control processes may become less effective at relatively high population densities (Fig. 3b), in which case outbreaks may erupt periodically. For example, spruce budworm, Choristoneura fumiferana Cramer, populations are thought to be controlled at low densities by the functional response of bird predators (Holming et al. 1977). However, when budworm populations attain high densities, the functional responses saturate because the avian predators become satiated. At this point, the efficacy of the predators in regulating budworm populations decreases with population density (i.e., they no longer act as a positive feedback, or inverse density-dependent, amplifying process). Another example can be found with the mountain pine beetle, Dendroctonus ponderosae Hopkins, which is restricted to individual weakened hosts by the resistance of the majority of the trees in the stand. However, the resistance of these hosts can be overcome if large beetle populations attack the trees en masse (Berrymon 1979a, 1979b). Hence, the regulating influence of host resistance disappears once...
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Biological Control, Thresholds, and Pest Outbreaks

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ABSTRACT

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Pest populations are frequently regulated below their potential levels of abundance by natural enemies, host resistance, or other biological interactions. However, if these regulating processes operate imperfectly, or if resistances vary in pest density, then we may observe periodic outbreaks of the pest. In effect, intolerant regulating processes create thresholds separating distinct dynamic behaviors, usually referred to as endemic and epidemic behaviors. If threshold functions can be defined in terms of measurable system states, then they offer a powerful approach for evaluating the risk of epidemics in managed ecosystems. Methods for defining threshold functions and constructing risk decision models are discussed.

Populations of many insect species are regulated at sparse densities for long periods of time by the action of natural biological control processes. This is particular noticeable in relatively undisturbed ecosystems, such as forests, but may also occur in highly artificial agro-ecosystems. Under these conditions, the insects are rarely considered pests because they do not normally exceed economic damage levels. However, on occasion, some of these populations may escape the influence of their controlling factors and erupt to high densities, wreaking destruction on humans, their crops, or forests (Fig. 1). Although these characteristics of pest outbreaks, or epidemics, have been recognized for many years, no general or practical framework has been presented for evaluating and predicting insect outbreaks. In the present paper I propose an elementary yet general model for describing eruptive insect population dynamics, and show how it can be applied to estimating outbreak probabilities.

Biological Control

For the purpose of our discussion, we will consider biological control to be the regulation of a population by any natural biological process. Thus, in addition to the usual examples of biological control of pest populations by parasites or predators (i.e., "control from above"), we also include the regulation of populations at low densities by host resistance or any other property of their plant. For example, most bark beetle populations (Colleoptera: Scolytidae) are prevented from reaching their potential abundance because of high resistance to attack in the majority of the trees in the forest (Berryman 1979a, 1979b). From this point of view, then, biological control is a result of trophic interactions between two or more species which maintain one or more of the populations at densities considerably lower than their potential. Support for this view can be found in the classical examples of biological control of introduced weeds and insect pests (see Clausen 1958, and Huffaker 1959).

Control Efficiency and Tolerance

Biological control processes are able to control pest populations because their negative impact on the population increases with pest population density. In other words, they function as negative feedback regulators of population density by imposing lower survival or reproductive rates on the population as its density rises (Fig. 3). If the control processes operate effectively at all population densities (Fig. 3a), then regulation will be maintained at all pest densities and outbreaks will never occur. However, some control processes may become less effective at relatively high population densities (Fig. 3b), in which case outbreaks may occur periodically. For example, spruce budworm, Choristoneura fumiferana Cramer, populations are thought to be controlled at low densities by the functional response of bird predators (Holling 1977). However, when budworm populations attain high densities, the functional responses saturate because the avian predators become satiated. At this point, the efficacy of the predators in regulating budworm populations decreases with population density (i.e., they no longer act as a positive feedback, or inverse density-dependent, amplifying process). Another example can be found with the mountain pine beetle, Dendroctonus ponderosae Hopkins, which is restricted to individual weakened hosts by the resistance of the majority of the trees in the stand. However, the resistance of these hosts can be overcome if large beetle populations attack the trees en masse (Berryman 1979a, 1979b). Hence, the regulating influence of host resistance disappears once...
the beetle population attains the critical density that enables it to colonize and start expanding into fresh territories in the stand.

The common characteristic of populations that are regulated for much of the time by biological control processes, but which exhibit periodic outbreaks, is that the control processes are intermittent to the complete range of population densities. Conifer defoliation processes, which are unable to operate effectively when bark beetle populations are large, and avian predators, which are ineffective at high densities of spruce budworms, are examples of intolerant control processes. Hence, tolerant control processes are those which maintain control irrespective of variations in population size (Fig. 3a), whereas intolerant ones are only able to maintain control within certain ranges of population density (Fig. 3b). The degree of tolerance is, of course, a critical factor in the effectiveness of biological control, and as we shall see later, tolerance can be severely affected by environmental factors.

Thresholds

One of the significant properties of population systems controlled by intermittent control processes is the presence of thresholds separating domains of different qualitative behavior (Berrymann, 1978a, 1981b). For instance, if we have a system where the control processes begin to lose their efficacy at a large natural population density, P, (Fig. 3b), then this produces a survival-reproduction curve which is periodic (dotted line in Fig. 4). The first equilibrium, S, can be shown to be potentially stable, whereas the second, U, is always unstable (Berrymann, 1978a, 1981b). This simple quasilinear model divides the system into two behavioral domains, controlled endemic behavior and explosive epidemic behavior. However, the exact value of the epidemic threshold, E, (Fig. 4) in other words, when the population density is such that the control process will be able to control the stable equilibrium, S, by the action of the biological control processes, but when it is greater than E, the control process can no longer control or even retard the increase in density of the system as a whole. (Berrymann, 1978b) for discussion of the complete cyclical epidemic cycle.

Assuming that the controlled population spends most of its time close to the stable equilibrium, S (i.e., S = F – X), then the tolerance of the control process can be expressed by T, where T 1 is the critical density P 1, being completely intolerant when P 1 ≤ 0 and becoming increasingly tolerant as P 1 → ∞.

Environmental Disturbances

Biological systems characterized by thresholds are extremely sensitive to environmental disturbances (Berrymann, 1981b). For example, suppose the system illustrated in Fig. 4 is at equilibrium, P 1, but then a change in the environment causes an increase in the pest population; e.g., windstorms creating a兰花 on A, a change in the density of coniferous pest populations raises above the unstable point P 1, then an explosive outbreak is initiated (Fig. 1). Alternatively, environmental disturbances can impose a stress on the control mechanism, reducing its tolerance to a point where P 1 is reduced to P 1, below the critical density of a forest stand, or an extremely harsh winter reducing bird population. It is further apparent that, although seasonal environmental disturbances may trigger a pest outbreak, a return to more normal conditions will often fail to terminate it, for by then the population may well be above the unstable threshold.

Threshold Functions and Risk

Two critical variables determine the qualitative behavior of pest populations: (1) the tolerance of the control processes, and (2) the density of the pest population. Thus, for any level of control tolerance, T 1, there will be a corresponding pest population density, P 1, which will define the threshold beyond which the pest population will increase from endemic behavior and, of course, P 1 will increase in direct proportion to T 1 (Fig. 5). For example, the density of bark beetles required to initiate an outbreak is inversely proportional to the average resistance of a forest stand, and higher spruce budworm densities will be required to saturate larger bird populations (Holling, et al., 1977, Berrymann, 1978b, 1981b). The threshold function, P 1 = f(T 1), is of considerable practical significance.

Defining Threshold Functions

Because threshold models can provide the manager with a powerful device for predicting pest population behavior and evaluating the risk of outbreaks, it is important to develop methods for defining these functions. Unfortunately there cannot be exactly specified. This is because they depend on transient states of a dynamic system which are rarely observed in real life. Therefore, we have to develop indirect techniques for approximating threshold functions.
The beetle population attains the critical density that enables it to colonize and establish healthy trees in the stand.

The common characteristic of populations that are regulated for much of the time by biological control processes, but which exhibit periodic outbreaks, is that the control processes are intermittent to the complete range of population densities. Conifer defoliation systems, which are unable to operate effectively when bark beetle populations are large, also predict predatory, which are ineffective at high densities of spruce budworms, are examples of intolerant control processes. Hence, tolerant control processes, such as those maintained in control as part of normal practices, may be tolerant to the complete range of population densities (Fig. 3b). The degree of tolerance is, of course, a critical factor in the effectiveness of biological control, and as we shall see later, tolerance can be severely affected by environmental factors.

Thresholds

One of the significant properties of population systems managed by natural control processes is the presence of thresholds separating domains of different qualitative behavior (Berrymann 1978b, 1981a). For instance, if we have a system where the control processes begin to lose their efficacy at a large natural population density, $P_0$, then this produces a survivorship-reproduction curve which includes a stable equilibrium (Fig. 4a). If the system is defined in terms of the average population size, $S$, and $T$, on the x-axis, the control process produces a survivorship-reproduction curve which includes a stable equilibrium (Fig. 4b). The first equilibrium, $S_e$, can be shown to be potentially stable, whereas the second, $U$, is always unstable (Berrymann 1978b, 1981a). This system's behavior divides the system into two behavioral domains, controlled endemic behavior and explosive epidemic behavior, for which $P_0$ is the threshold (Berrymann 1981b). In other words, when the population density is below $P_0$, the system's behavior will be toward the stable equilibrium $S_e$ by the action of the biological control processes, but when it is greater than $P_0$, the system is not only controlled but also becomes a predator-prey population, the predator-prey dynamics, or the viability of the habit for these organisms may be reasonable variables to choose.

Having identified the variable(s) that determine control, the next step is to observe the system in both behavioral modes and under different conditions of the control variable(s). For instance, by observing a large number of trees of variable resistance, Waring and Pitman (1980) were able to identify the threshold mountain pine beetle attack density required to kill individual lodgepole pines (Fig. 5a). An alternative method is to construct a realistic model of the beetle-host interaction and identify the threshold by simulation (Fig. 6). Simulation models are a valuable tool in the study of the system's behavior and can be used to identify the threshold by simulation (Fig. 7). Thus, the relationship between threshold functions and catastrophe manifolds has been discussed previously (Berrymann 1978b).

Two critical variables determine the qualitative behavior of beetle population: (1) the tolerance of the control processes, and (2) the density of beetle population. Thus, for any level of control tolerance, $T$, there will be a corresponding proportion of beetle population density, $P$, which will define the threshold for endemic from epidemic behavior and, of course, will increase in direct proportion to the average resistance of a forest stand, and higher spruce budworm densities will be required to saturate larger beetle populations (Holling et al. 1977, Berrymann 1978a, 1981b). The threshold function, $F = f(T)$, is of considerable practical significance.
easily measured stand variables.

Conclusions

The idea of invertebrate biological control processes giving rise to thresholds separating endemic from epidemic behavior forms a strong qualitative theory for the dynamics of eruptive pest populations. The theory has potential applications in pest management decision making, particularly in evaluating the risks of pest outbreaks in managed ecosystems. Risk decision models can be constructed provided the tolerance of the control processes or their ability to absorb random changes in population density, can be expressed in terms of measurable variables (e.g., host resistance factors or predator or parasite population density) and if the density of the pest population can be measured, or expressed as a function of other system variables (e.g., phloem thickness, weather, etc.). Given these preconditions, threshold functions can usually be estimated empirically. Risk decision zones can then be drawn to reflect the variability of the environment and the risk aversion of the pest manager. Interestingly, the theory of invertebrate control processes and behavioral thresholds may have much broader applications in the biological sciences. Nervous breakdowns, epileptic seizures, and aggressive outbursts may all involve the breakdown of invertebrate control processes due to stimulus overload or external environmental stresses. Thus, the approaches developed in this paper may also be applicable in evaluating the risks of abrupt behavioral changes in individuals, nations, and societies.

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1978a. A synthetic model of the lodgepole pine forest.
Fig. 6.—(a) Threshold attack densities of the mountain pine beetle required to kill lodgepole pine of varying resistance (,std. trees; O, live trees; redrawn from Wardle and Fitman [1980]). (b) Threshold beetle population densities required to initiate an epidemic in homogeneous lodgepole pine stands of varying resistance (test. stands/epidemic stands; random stands; simulated data from a computer model after Raffa [1980]).

easily measured stand variables.

Conclusions

The idea of insect control biological control processes giving rise to thresholds separating endemic from epidemic behavior forms a coalesce qualitative for the dynamics of eruptive pest populations. The theory has potential applications in pest management decision making, particularly in evaluating the risks of pest outbreaks in managed ecosystems. Risk decision models can be constructed provided the control processes or their ability to absorb random changes in population density, can be expressed in terms of measurable variables (e.g., host resistance factors or predator-prey population density) and if the density of the pest population can be measured, or expressed as a function of other system variables (e.g., phloem thickness, weather, etc.). Given these preconditions, threshold functions can usually be estimated empirically. Risk decision zones can then be drawn to reflect the variability of the environment, and the risk aversion of the pest manager.

Interestingly, the theory of insect control processes and behavioral thresholds may have much broader applications in the biological sciences. Noxious outbreaks, epidemic seizures, and aggressive outbreaks may all involve the breakdown of insect control processes due to stimulus overloads or external environmental stresses. Thus, the approaches developed in this paper may also be applicable in evaluating the risks of abrupt behavioral changes in individuals, nations, and societies.

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