ECOLOGICAL BASES FOR BIOLOGICAL CONTROL

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ABSTRACT - The ecological bases of biological control are reviewed, and, in particular predation theory and predator searching patterns. Recent literature suggests that many of the common rules of thumb used in biological control of insect and plant pests do not fully follow established dogma. Furthermore, we question the ecological stability of large scale microbiological pest control, which we find to be evolutionarly risky, leading to the rapid appearance of resistant pests. In fact, we argue that microbial control as currently practiced differs little from standard chemical control programs, due principally to the lack of epidemological understasnding of the system being worked. Recent findings based upon hierarchy and percolation theory may allow us to explain why some biological control programs do not work, as well as explain the apparent discrepancy between small scale field tests and large scale liberations. Chief among the current problems are integrating spatial and temporal scales of variation into theoretical strategies of natural enemies, both behaviorally and evolutionarly.

Index terms: theory, percolation, behavior, optimization; parasitoides; predators; diseases

BASES ECOLÓGICAS DO CONTROLE BIOLÓGICO

RESUMO – As bases ecológicas do controle biológico são revistas, em particular a teoria da predação e os padrões de procura dos predadores. Literatura recente sugere que muitas das regras práticas usadas no controle biológico de insetos pragas e plantas daninhas não seguem completamente os dogmas estabelecidos. Além disso, nós questionamos a estabilidade ecológica do controle microbiano de pragas em grande escala, que julgamos ser evolucionariamente um risco, capaz de levar a um rápido surgimento de pragas resistentes. De fato, nós argumentamos que o controle microbiológico da maneira como é praticado difere pouco dos programas de controle químico praticado atualmente, devido principalmente a falta de conhecimentos epidemiológicos dos sistemas que estão sendo trabalhados. Recentes descobertas baseadas na teoria da percolação e hierarquia podem nos levar a explicar por que alguns programas de controle biológico não funcionam, bem como explicar a aparente discrepância entre teste de campo em pequena escala e as liberações em larga escala. O principal entre os problemas correntes é a integração das escalas de variação espacial e temporal dentro das estratégias teóricas dos inimigos naturais, tanto comportamentalmente como evolucionariamente.

Termos para indexação: percolação, comportamento das pragas, otimização, parasitóides, doenças, predadores.

INTRODUCTION

Classical biological control is one of the most cited examples of applied ecology (Odum 1959). As in any type of pest control, the objective of biological control is to reduce the population of an organism, perviosuly defined as a pest, below established economic thresholds principally through cost-benefit analysis when compared with alternative control strategies (Geir 1966). However, classical biological control deals with population regulation, and not only its drastic immediate reduction (Romagnano & Fowler 1988). Only three ecological process are known to regulate populations: self-regulation, competition, and predation

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sensu lato, but only the last two have potential of human manipulation (Fowler et al. 1987). Thus, biological control uses ecological processes to attain economic goals. But, is ecological theory really applied when classical biological control is conducted? In this paper, we review some of the theoretical tenants of population regulation, the new mathematical and empirical findings, especially with common rule of thumb procedures used in biological control, and we risk to suggest that newly opening areas of ecological theory have much to bear on how and why biological control operates.

THE ECOLOGICAL WEB

If we consider that the living world is organized into food webs (Fig. 1), we canbegin to approach those concepts necessary for understanding the ecological processes at work in biological control programs. In spite of the large number of insect and plant species present in the world, only certain combinations of species associations in fact exist. This is the end result of selective processes, irespectively if we are dealing with insect-plant, host-parasitoid, or host-disease loops (Caswell, 1976)

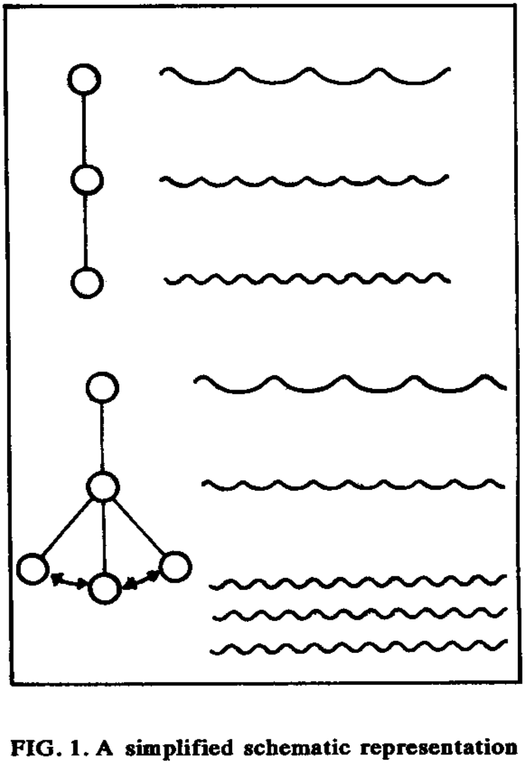

FIG. 1. A simplified schematic representation of regulation through trophic levels in food chains and webs. In food webs, horizontal arrows represent competitive processes.

The limitations produced by selection have led to niche differentiation among the members of our evolutionary play. For example, by introducing an exotic crop we hope to achieve a good productivity. However, if an exotic pest of this plant is accidentally introduced, or if a native pest adapts to this plant, then we have serious problems because we have not completed the levels of the food web. In the first case, those exotic natural enemies which held the pest in check in its coevolved homeland are not present. In the second, by moving the ecological settings,the pest escapes from its coevolved natural enemies which are using the previous cues needed to find the pest. In other words, both situations lead to vacant niches (Lawton 1982), which classical biological control seeks to fill.

POPULATION REGULATORY PROCESSES

Our conception of how species systems function in centered upon the idea of equilibrium. Although populations may fluctuate widely (Fig. 2), even those populations that have apparently irregular fluctuations can be deterministically described by chaotic models. The characteristic extremes reached by certain pest species can be translated into varying degrees of damages, which form our criteria decision making in integrated pest management programs. However, our paradigm in biological control, is that we can reduce levels and under proper conditions maintain these at lower equilibrium levels through the action of natural enemies.

This implies that population fluctuations are controlled through negative feed-back loops, which are the ecological processes of competition, predation, or auto-regulation (Fig. 1). Indeed, we can find evidences that these negative feed-back loops do indeed exist in nature (Figs. 2 & 3).

The overwhelming consensus of modelers of interactions of hosts with their natural enemies for many years was that spatial heterogeneity, and, in particular the aggregation of attacks in high density host patches, were necessary for stabilizing the interacting populations (Hilborn 1975; Hassell 1980, 1982; Anderson & May 1978; Fowler 1989). Implications for biological control are that natural enemies should concentrate search in areas of high host density (Cook & Hubbard 1977; Hassell 1978). Beddington, et al. (1978) based upon a series of Nicholson-type models (Bailey et al 1962), concluded that "the patchy distribution of the host and the differential exploitation of these patches by the" [natural enemy] "provide the key to most cases of successful biological control".

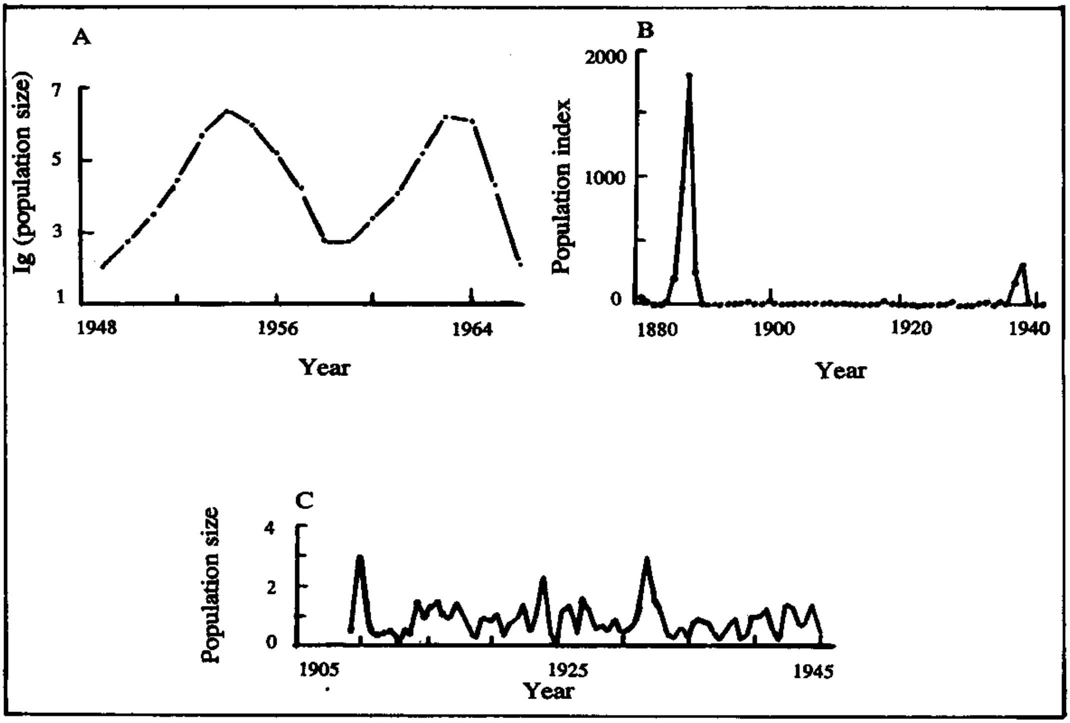

FIG. 2. Varying population fluctuations found in Lepidoptera: [A]. *Zeiraphera diniana* varies over 4 levels of magnitude at periodicities of approximately 10 years; [B]. *Dendrolimus pini* hits large populations levels infrequently; [C]. *Chilo suppressalis* fluctuates around a constant level.

However, we know little of how parasitoids, predators and diseases really forage in nature. We usually use inferences based upon field collections in which we evaluate percent parasitism or disease

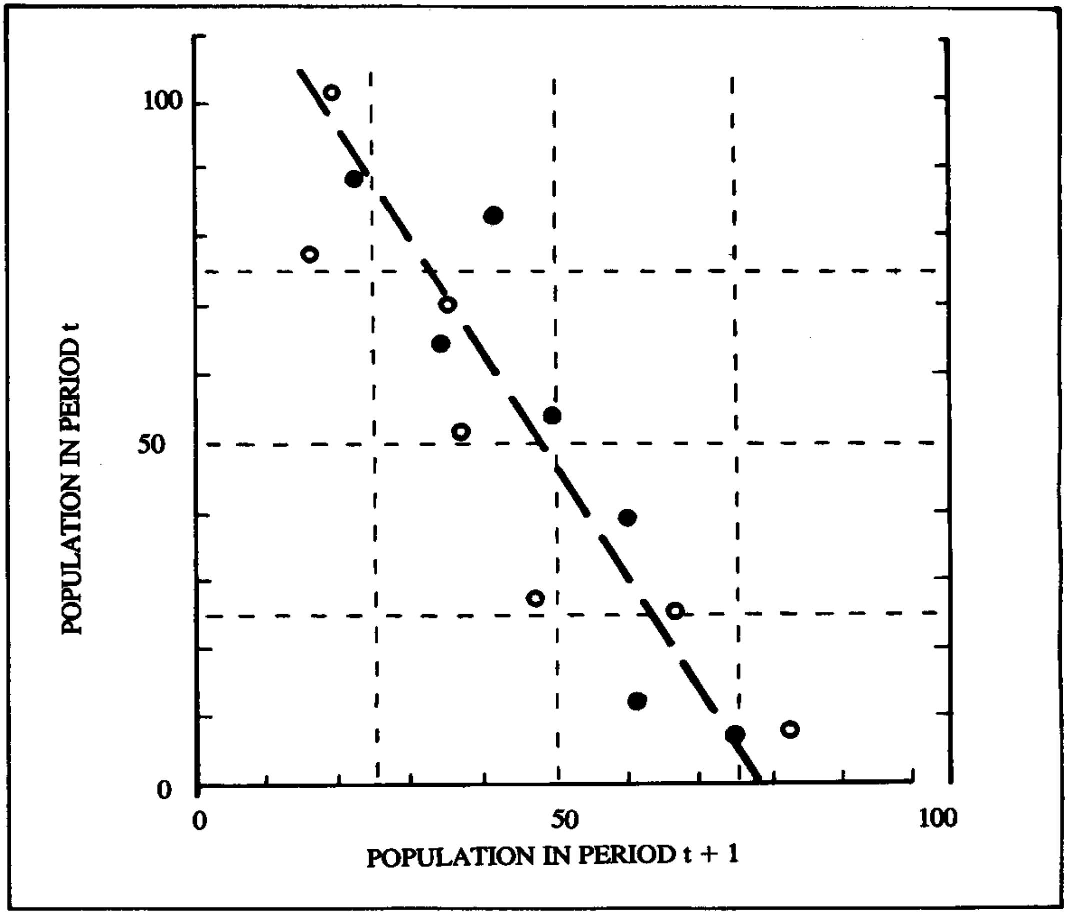

FIG. 3. A typical example of population regulation as ascertained through field sampling. A negative auto-correlation should be found between population estimates taken at successive time intervals. The example shown is for *Scapteriscus borellii* (after Fowler, 1989).

[predation and herbivory escape this analysis (Heads & Lawton 1983; Hassell 1980; Lessels 1985; Fowler 1989). Chesson (1982) cautions about using data of these type for inferring searching patterns of natural enemies.

We should also consider a further complication in trying to effectively use classical biological control agents. Many pest species move aggregation patterns in response to natural enemy presence (Fowler 1988; Fowler & Garcia 19789); Weiss, 1982) If we are searching for a natural enemy that we hope will be able to effectively attack a pest species with a known spatial dispersion, we may find that when introduced, the presence of the natural enemy changes spatial patterning, leading to another failure. This type of reasoning has never been fully discussed in the literature, and failures are generally attibuted to other causes.

Enhancement of regulatory processes

Price (this volume) comments upon the effects of succession, resource usage amplitude, and population dynamics on the successes of classical biological control. However, there are other types of non-agricultural situations in which competitive displacement of a pest species would be desirable by another organism, or group of organisms through diffuse compettion, which have characteristics not considered detrimental. Examples may be found in certain types of veterinary and public health situations (if larval and not adult competition is important), and for some of the pestiferous social insects.

No documented cases of competitive displacement for public health or veterinary pests can be found. However, there are a number of pests which should be subject to population reduction through competition. These include the *Biomphalaria snails* (Romagnano & Fowler 1988), and feces and water breeding flies. In all of these cases, the only attempts to biologically control their populations has been through the liberation of predastors and parasites, and or the use of pathogens.As we commented in the opening portion of this paper, interspecific competition leads to the same ecological result as predation. Although the true impact of competition on population regulation is still a hot subject of debate, our manipulation of interspecific competition has been crude. Even the introductions of predators, parasites, or pathogens may affect competitive interactions, and it would be interesting to know how many of the recorded successes are due to a tightening of competition following populations reduction by a classical biological control agent. Obviously, this means that we must fully understand the system before liberation, and then follow-up with studies after liberations, be they augmentative or one-shot.

As a possible example, we provide our studies on the effects of phorid flies on fire ants *Solenopsis*. These flies only parasitize the larger workers, and under no circumstances could the liberation of phorids lead to their biological control. Or could it? Fire ants are extremely oportunistic when exploiting food resources. After a scout ant finds a food item, it recruits a large number of workers to the item. The major workers principal function is to protect the food item from usurpage by other ants, either of same or different species, while the smaller workers cut it into pieces to take to the nest. When phorid flies are present, larger workers flee and hide under grass blades, leaves, or similiar shelters to avoid parasitism, and the food item is then rapidly stolen by a variety of other ant species. In this case although parasitism is extremely low, because of the behavioral modifications that the phorids cause, fire ants are unable to fully exploit an available food item. As food is presumably transformed into the production of more ants, the fire ants are competitively at a disadvantage, especially if food is transformed into the production of new sexuals for colonization.

We still do not know if this fly will be an effective control agent of introduced populations of fire ants in the United States or Caribbean, but this is due principally to the fact the community matrix into which fire ants are inserted is not the same as we have in Brazil. The effects could be more dramatic, less dramatic, or nill. Until we understand more about the oragnization and structuring of communities, we are unable to even guess as to the possibilities. However, this example demonstrates that our thinking along the classical lines of biological control may not fully resolve a complex ecological problem.

The enhancement of competition through stress is also a common phenemon in weed control. Here, space and nutrients are the limiting factors, and through stressing weed species through herbivory or disease, we are able to enhance the competitive ability of the crop or grass of economic interest. Thus, we find that the same ecological processes are operative, irrespective of whether the organism in interest is vegetal, animal, and perhaps even microbial.

However, enhancement processes may also reduce effectiveness of biological control agents. To illustrate this, let us consider nematophagous fungi. We have documented the loss of effectiveness of the entomophagous nematode *Steinernema scapterisci* in *Scapteriscus borellii* due to the fact that nematophagous fungi are found associated with mole cricket cuticles in areas in which these nematodes exist. Although these nematodes are efficient control agents of mole crickets, when mole crickets have hitchiking fungi, nematodes fail to control a large portion of the population (Fowler & Garcia 1989). In fact, the fungal population increases to such levels that the nematodes are completely erradicated at local levels. Such a response, expected under ecological theory (Fig. 1) may lead to the necessity of augmentative releases of soil nematodes for soil pest control,due to the fact that the natural regulation of these nematodes by other elements of the soil biota is nature]'s way of regaining control. Many other situations of ecological responde to man's manipulation will undoubtedly be documented as we seek to explain the failures of systems which we thought should be globally stable and leading to classical biological control.

EXOTIC VS. NATIVE PESTS: THE BASIS OF CLASSICAL BIOLOGICAL CONTROL

Exotic organisms have always been the prime targets of classical biological control. If an exotic crop is introduced, such as *Citrus*, soy-bean, sugar-cane, coffee, etc., there is a high probability that its principal pests will also be exotic and from the same geographical origen. Given the coevolved nature of food chains, if an element is missing, such as a parasitoid which attacks a herbivore, the populations of this latter will attain levels much higher than those possible where the parasitoid is present, producing losses much more severe than those experienced in the geographic origen. Most of our major successes in classical biological control have evolved introduced natural enemies attacking introduced pests (Clausen 1978; Hokkanen 1985). Our successes in using exotic natural enemies for native pest species is much lower (Carl 1982). These facts are attributed principally to the coevolution and specificity of the host-natural enemy system.

However, Dennill & Moran (1989) have called attention to the fact that perhaps many of our criteria of selectivity used for classical biological control, and particurlarly of weeds, indicate that a high degree of selectivity may not be always desirable, and that new associations of natural enemies with hosts do not necessarily result in polyphagy on the part of the natural enemies.

Although our criteria of deciding which natural enemy should be used for the control of a given pest species should not be drastically modified, we are beginning to witness the questioning of dogma, and the future should be revolutionary. However, until we understand more about ecological systems, the major effort of biological control will continue to be the supression of exotic pests.

SPATIAL AND TEMPORAL SCALES; HETEROGENEITY, HOMOGENEITY AND THE MANNERS WE INTERPRET PHENOMENA

In textbooks of biological control, and indeed in many of its published accounts little mention is made to the spatial and temporal scales of the phenomena we are examining, whether it be parasitism, predation, epidemology, etc. However, given the new focus of integrating scales in ecology (Allen & Starr 1982), we should also examine how our perception of what is happening changes as we vary our spatial and correlated time scales.

If we go back to classical theory, we should expect that a phenomena that is locally stable to be regionally unstable (Murdoch & Oaten 1975; Rose & Harmsen 1981), and its inverse is true. But, what does this mathematical truism mean in every day field ecology? First of all, many of our systems tested at small spatial scales over also short time spans give us differing results than those of longer time scales or larger spatial scales. This leads to varying interpretations of response by natural enemies to host density, as discussed previously.

However, if we concede that the environment is patchy, that the responses of plants and their herbivores, and of the natural enemies of these herbivores is superimposed upon this template to create even further spatial heterogeneity, then perhaps we need new methods to understand processes. Chief among processes leading to spatial heterogeneity is perturbation (Rykiel Junior 1989. In agricultural situations, most of our techniques impact upon both pest and non-pest populations.

New methods are now emerging to allow us to evaluate changes of scale on ecological processes. Among the most promising are fractal geometry (Orbach 1986) and related percolation theory (Stauffer 1985). To illustrate the applicability of these methods, let us assume that the habitat, be it an agricultural crop, a forest, etc., can be divided into many quadrants. Let us suppose, based upon what we know of spatial heterogeneity, that not all of these quadrants have a pest present. Even if a pest is present at a known density, not all of these will be susceptible to attack by a natural enemy (Hassell & Anderson, 1984). We could then assign a probability value of density-susceptibility to each quadrant which would indicate the chance of a natural enemy finding and attacking hosts. These are the classical chacracteristics of traditional population models until now. However, let us consider the probability that a natural enemy will be able to cover an area from one side to another. Results from percolation theory (Table 1) illustrate such an analysis. These results, coupled with information on the behavior of the natural enemy and on the aggregation of hosts in the field may explain why some classical biological control programs are successful, and why others depend upon augmentative releases to function, such as *Cotesia – Diatrea* in São Paulo. Perhaps our criteria based upon small scale experiments or laboratory evaluation do not fully reflectthe reality of the world lived by both host and natural enemy (Fahring & Merriam 1985; Fahring & Paloheimo 1988).

TABLE 1. The critical probabilities of percolation in a plantation cropping system with a randomly distributed pest, and the number of patches, N_{patch}, explored by a parasitoid, or colonized by a pathogen, per unit time. P_{pest} are the proportions of patches with pests necessary for the parasitoid or pathogen to spread spontaneously across the area, assuming that they explore an area of N_{patch}.

N_{patch}	P_{pest}
1	0.5928
25	0.0353
100	0.0089

BIOLOGICAL CONTROL AND CONTROL USING BIOLOGICAL AGENTS: A NON EXISTING EQUIVALENCE

As the reader may now have gleaned from our philosophical basis, what many people consider as biological control (=microbial and/or augmentative release programs) is to our thinking not true biological control. Our reasoning is that application technologies must be developed and we only substitute chemical agentes tor biological agents.

However, this does not imply that microbial agents cannot be used in classical biological control programs, but rather that we must understand the ecological processes involved, such as epidemology and the effect of spatial heterogeneity (Fowler, 1989). Once again, we need information on effects at various spatial scales to fully understand how to effectively employ microbial agents without risking the creation of resistent pests through massive, large scale applications of bioinsecticides.

CONCLUSIONS

We have tried to briefly review some of the necessary ecological theory needed to fully understand how and why classical biological control functions. At the same time, we have called attention principally to a deeper knowledge of behavior, and processes leading to and adapting to spatial and related temporal heterogeneity. We predict that a deeper understanding of population dynamics necessary to fully understand the maintenance of food webs, which practioners of classical biological control manipulate, can only be resolved when we begin to integrate scales.

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