

PARASITES

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INTEGRATED CONTROL signifies the selection and use of various methods of applied control to harmonize with the natural control factors already operating. It cannot be applied until the roles and relative importance of these natural control factors are known. The prerequisites to its use are a knowledge of both basic ecological principles and the ecological features that are specific to each target species. The goal is to achieve the minimum degree of damage to the product that is consistent with both minimum damage to the environment due to side effects of control measures and maximum long-term economy. These side effects, primarily due to insecticides, are now well known: (1) development of resistance, (2) resurgence of treated populations, (3) outbreaks of secondary pests, (4) contamination of the environment by persistent poisons, and (5) destruction of beneficial species.

Objectives of Biological Control Programs

In the past, the degree to which a biological-control operation has been considered successful has been judged on the extent to which the introduced agents have provided the ultimate in control—the permanent maintenance of a pest's abundance below the level of economic injury. For example, DeBach (1964) differentiates between outstanding success, substantial success, and partial success. The assessment of a particular case is made on the basis of: (1) the proportion of the total range of the pest in which control is achieved, (2) the degree to which the duration or severity of outbreaks is reduced or the duration of the

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intervals between outbreaks is increased; (3) whether supplementary control methods must be used, and (4) whether a pest is of great or slight economic importance.

It has been suggested, for example by Prebble (1960), that with certain types of pests where only very high densities cause appreciable damage, a program might be deemed fully successful if the degree of economic injury is significantly reduced even though less severe and less prolonged outbreaks still occur.

The biological-control program against the gypsy moth can be cited as an example where the evaluation of degree of success would depend on what the original objective of the program was considered to be. DeBach (1964) rated it as a "partial success" even though Clausen (1956) said that the end result in America was that outbreaks were reduced to a level "comparable in range and severity" to those occurring in Europe. If this degree of control had been set originally as a realistic objective, then the final rating might have been a substantial or even an outstanding success. In this program the effectiveness of the introduced agents has undoubtedly been inhibited by the continuing and widespread use of insecticides against the pest.

Although biological-control specialists have long recognized the importance of partial control, some of the early spectacular and complete successes have encouraged the setting of impossibly high standards for judging the usefulness of biological-control attempts. Such standards discourage attempts aimed toward partial control, which could reduce the frequency, severity, or duration of damage. Prebble (1960) criticized this all-or-none attitude toward control operations as being incompatible with our increasing knowledge of population dynamics and forest ecosystems; but the attitude still persists.

Philosophy Underlying Biological Control

Biological-control workers have stressed the importance of governing factors in the total complex that restricts population increase. Governing factors are defined as those that are affected by changes in population density and, as a result, modify their influence so as to oppose population change (Nicholson 1954). However, many factors to which the above definition of

governing can be applied, are restricted in their ability to influence population change. These factors may have a limited ability to respond to large increases in density and operate only in endemic populations. Certain parasites of spruce budworm (Miller 1963) and elaterid predators of the pine looper (Turnock 1969) are examples. Other factors such as diseases may operate only at high densities.

The relative importance of parasites that are effective at low host densities versus those capable of reducing outbreak populations is one that cannot be answered on the basis of available information on population dynamics. The most effective parasite species would be capable of operating effectively both at low host densities and under outbreak conditions. Certainly some parasites that are capable of terminating an outbreak are also effective at low densities: *Cyzenis albicans* and *Agropyron flaveolatum* on the winter moth in Nova Scotia (Embree 1965); *Agathis pumila* and *Chrysocharis laricinellae* on the larch case-bearer in eastern-central North America; *Olesicampe benefactor* on low larch sawfly populations in alpine Europe and outbreak populations in Manitoba. On the other hand, the collapse of the original European spruce sawfly outbreak in North America was caused by an introduced virus, while subsequent outbreaks have been controlled by the combined influence of the virus and two parasite species, or, in some cases, either virus or parasites acting alone. The parasites are particularly effective at very low host densities and are sensitive to minor fluctuations at these levels (Neilson *et al.*, *in press*).

We suggest that, wherever a particular biotic agent has the capability of maintaining population levels permanently within given limits of abundance that are non-damaging, the qualifying word "effective" be used to describe it. Such agents are effective as long as the non-governing mortality factors show no marked deviations from their long-term average influence.

It seems probable there may be situations in which a complex of governing factors, none of which by itself is an "effective governing agent," act together in such a way as to be effective. The possibility of "stacking" a number of partially governing agents to attain effective control requires more study. A basic

cleavage of opinion exists as to whether or not a single introduction of the best possible parasite species is preferable to multiple introductions. Though while the introduction of competing species may be detrimental to the more efficient of the two, i.e., the case of *Eulimneria rufifemur* interfering with *Orgilus obscurator* attacking the European pine shoot moth (Pschorn-Walcher et al. 1969, Syme in press), such examples cannot be automatically extended to reach the conclusion that a single parasite species will be more effective than several species.

Non-governing factors such as weather may be necessary components of processes that are density-dependent in action. For example, when the average degree of protection afforded by living places decreases as population density increases, percentage mortality due to adverse weather also increases. Similarly, crowding phenomena may render individuals more susceptible to adverse weather by changing their behavioral and/or physiological characteristics.

Insecticidal applications usually correspond in their effect to the catastrophic mortalities that occur when weather conditions are severe. Since they are normally applied only at very high densities of the pest, they are density-dependent to a degree. Their application, however, may elicit the sort of homeostatic mechanisms that force the pest to remain at high densities most of the time (National Academy of Sciences 1969). The spruce budworm outbreak in south-central New Brunswick apparently illustrates this situation: since 1960, an average of over 1,600,000 acres has been sprayed annually to minimize tree mortality. Although this objective has been attained, the outbreak continues and surveys indicate that 10 million acres will be defoliated in 1970 (70 percent of them will have moderate to severe defoliation) and plans are under way to spray about 3 million acres.

It should be possible to use insecticides in a density-governing way by interposing man as the controlling component to create a feedback loop. In such a case the application of insecticides would be varied in time, space, and intensity to stabilize population levels rather than to produce high mortalities. Man

may also be able to achieve such results by regulating microclimates; for example, the humidity in tree nurseries or plantings could be modified to vary the intensity of mortality due to disease. Other control methods that could be utilized in a governing way through human intervention are: the use of anti-feedants, repellents, pheromones, chemosterilants, radiation sterilization, electromagnetic energy, and behavioral or genetic manipulation.

It has been implied above that the reason most pest species are pests is because there are no effective governing processes acting against them. Even with pest species, however, certain governing processes eventually come into play if density continues to increase, namely those connected with food shortage, or reduced fecundity or viability. Below such density levels it is likely that non-governing processes connected with weather, food quality, etc. are major determinants of annual changes in population level.

Among the reactive factors it is parasites, invertebrate predators, and diseases that are considered to have a special potential for governing populations. Although their functional responses and "behavioral numerical responses" (*sensu* Buckner 1966) may be of considerable importance, particularly at lower levels of host density, their most important characteristic is that their "breeding numerical response" (*sensu* Buckner 1966) is potentially limited only by host density and is not restricted by factors such as territorial behavior.

The breeding numerical response of a particular species is probably at least partly dependent on its functional response (i.e., if there is an increase in the number of hosts attacked per parasite with an increase in host density, this results in an increase in the ratio of adult parasites to adult hosts in the next generation). In order for the agent to exert a governing action, the total response during one or more generations to an increase in host populations must result in a sufficiently large increase in mortality to cause a reversal of the population trend. The behavioral numerical response of avian predators to concentrations of insect prey certainly increases prey mortality (Buckner and Turnock 1965; Mattson *et al.* 1968), but its effect-

tiveness as a governing factor is not well documented.

In the control of the Klamath weed by *Chrysolina quadrigemina* in California and the prickly pear cactus by *Cactoblastus cactorum*, the phenomenon of local annihilation of both host and agent has occurred. This has been followed by re-invasion; first by the host and later, sometimes after an interval of sufficient duration to allow the host to build up appreciably, by the agent. Huffaker and Messenger (1964) state that following re-invasion of the Klamath weed, a great variety of forces (rain-fall, temperature, fire, etc.) may devastate or destroy these stands in the absence of the beetle. A population-dynamics study in such stands during this period would show that physical factors would be of major importance in determining annual changes in population levels. They state, however, that the beetle still holds the key role since whenever stand densities become threateningly high the beetle invariably arrives by dispersal from residual populations elsewhere and drastically reduces or annihilates these populations. The true role of the beetle could be determined only by a long-term population-dynamics study.

It is not known how important local annihilation and resulting fragmentation of host populations is when insect pests are controlled by biotic agents, but it is obviously worthy of considerable study. Wolcott (1958) cites two examples where biological control of pests in Puerto Rico was too successful, resulting in the disappearance of the agents from the island and the later reappearance of the pests, but not the agents. In continental areas the phenomenon may be of relatively common occurrence, particularly with hosts against which biological control has been successful; but if the local annihilation occurs over a comparatively small area and is of relatively short duration, it would be difficult to detect. Andrewartha and Birch (1954) believe it is going on around us all the time, although due to underpopulation phenomena rather than to excessive kill by biotic agents, whereas Varley and Gradwell (1970) believe it is not common in the field.

At the borders of distribution of some species, environmental pressure may be so severe that only temporary existence is pos-

sible, and it is usually only in the more optimal areas that a pest species periodically increases to excessive numbers. In the intermediate areas the species may be a relatively permanent occupant, but its numbers rarely rise to injurious levels. In these areas it probably becomes extinct periodically, and populations are re-established by immigration from the optimum zone. If the only effective governing processes in the optimum zone are those connected with depletion of the food supply, we should not expect to find other governing processes in the intermediate areas where, because of the lower densities of host, there is no competition for food. A possible example of such a species is *Bupalus piniarius*, which is a serious pest in Germany, England, etc., where it is limited mainly by food depletion. A thorough population-dynamics study of low-density populations in Holland (Klomp 1966) failed to reveal the presence of an effective governing homeostatic mechanism.

It has long been postulated (Nicholson and Bailey 1935) that a delay or lag in the response of a parasite or predator to an increase in host density gives rise to coupled oscillations of host and agent that increase in amplitude with time and are inevitably self-destructive. Varley and Gradwell (1970) state that only specific and synchronized enemies act in this way. This would suggest that such specific enemies would not be effective biological control agents. Support for this view is given by the conclusion of Liu Chung-lo (1962) whose analysis of 30 successful attempts indicated that moderate polyphagy will better ensure success than monophagy. On the other hand, Doutt and DeBach (1964) conclude that most successes in biological control have resulted from the introduction of rather host-specific entomophagous species having good synchronization.

Klomp (1966) states that oscillations of increasing amplitude are never observed under natural conditions because they would lead to extinction. However, such oscillations might occur in nature under unusual circumstances such as the introduction of a specific, well-synchronized parasite. This may have occurred in Puerto Rico, where the extinction of two entomophagous species was observed. The lack of observations of this phenomenon may be related to its ephemeral nature: either the system is

stabilized or extinction occurs rapidly.

Coupled oscillations of increasing amplitude can be stabilized into coupled oscillations of approximately constant amplitude by damping mechanisms. As a generality, a damping mechanism can be any interference component that reduces the efficiency of enemies as prey density increases. Varley and Gradwell (1970) concluded from a study of models that it is impossible to mimic the coexistence of two specific parasites unless each is provided with its own density-dependent mortality. Huffaker and Kennett (1969) present data indicating that the effective area of discovery (searching capacity) of the ichneumonid *Venturia canescens* decreases as host density increases, and this would tend to dampen oscillations because the parasite is acting as its own density dependent factor.

Do the results of population-dynamics studies lend support to the above views? Studies on defoliators that occasionally reach very damaging densities, such as the spruce budworm (Morris 1963), the lodgepole needle miner (Stark 1959), and the larch sawfly (Ives *et al.* 1968), indicate that the determination of density levels below those causing food shortage is usually due to climatic causes or non-governing biotic agents. There are certain biotic agents that seem to become abundant only after very high densities are reached; and although these may play an important role in decreasing the duration of outbreaks, they are not effective in terms of governing—i.e., preventing the excessive increases in host density in the first place.

Some species that have been studied intensively have been shown to have their densities at all levels determined mainly by parasites. One of these is the black-headed budworm in the Maritimes (Morris 1959; Miller 1966) which, in this region, occasionally reaches high densities for short periods. Miller concluded that population release was associated with years of low parasitism and favorable weather, while population decline was associated with late larval parasitism. This defoliator has caused mortality of western hemlock on the West Coast, and a population analysis in this area might show a basic difference in the population-level determinants as compared to the Maritimes. Varley and Gradwell (1970) caution that in Morris's analysis,

parasitism is causally responsible for rather less than half of the population change, even though estimations of parasitism in year N allow a reasonable prediction of population density in year $N+1$. This is because the residual mortality varies in a way similar to variations in larval parasitism, and these authors believe that the unstudied aspects such as parasites or predators acting in the egg or pupal stages contain a major cause of host density fluctuations. They believe an identical situation occurs in the case of the grey larch moth (*Zeiraphera diniana* Gn). Concerning this latter species, however, Auer (1969) concluded, from an analysis using a five-factor model, that, within the optimal area, "The biological and density-dependent actions are much more efficient than the abiotical actions." Preliminary results of a study of the fall webworm (Morris 1969) indicate that American populations are maintained at a low level mainly by the effects of heat accumulation on survival. However, he suggests that simulation studies using a biologically meaningful model, now in preparation, will be necessary to determine the role of density dependence in the webworm's system of regulation.

The results of these studies give conflicting answers to the question of whether effective governing factors maintain the low densities of non-pests. Many studies have documented the absence of effective governing factors during epidemics of pestiferous species which, at such times, can be aptly described as out of control. There have been too few attempts to identify the presence of such factors in species that have never been pestiferous. Comparative studies of population regulation of pests under both endemic and epidemic conditions are necessary for the development of rational pest management.

Classification of Pestiferous Species

The "classical" approach to biological control was initially developed when it was realized that exotic pests commonly lacked the natural agents that prevented their depredations in their place of origin. Unfortunately, however, the idea that biological control consisted solely of the introduction of enemies from foreign lands has tended to dominate discussions of the

potential of biological control (e.g., *Simmond's 1956 critique of Taylor 1955*) to the detriment of consideration of alternate approaches and emphasis on the need to fit the approach to the characteristics of the target species.

There are different types of pests that vary in their susceptibility to the classical approach, and in this paper we recognize four categories of pest insects that differ in their origin, the mechanisms that determine their population levels, or the relative densities at which damage occurs.

1. *Exotic pests*: species originating from other regions, which lack the effective governing mechanisms that are present in their native habitat.
2. *Anthropogenic pests*: species whose populations reach damaging levels due to changes made in the environment by man's activities.
3. *Opportunistic pests*: species with a "wide-amplitude" type of population behavior (*Watt 1968*), which periodically reach very high densities in response to favorable environmental conditions.
4. *Low-density pests*: species that occur at low densities, apparently due to the action of effective governing mechanisms, but nevertheless cause economic damage.

Exotic pests have traditionally been considered the most promising targets for biological-control operations because, in their native habitat, they occur at non-economic densities, presumably due to effective governing mechanisms. Living biotic agents are important components of governing mechanisms, and these agents often can be transported and established in the invaded region.

Anthropogenic pests resemble exotic pests in that they are effectively governed in some areas, but differ in that they are not effectively governed in habitats that have been greatly modified by human activity. Since effective biotic agents usually exist in adjacent undisturbed areas, these modifications appear to have created an environment that limits the effectiveness of these agents. Biological control through colonization is therefore un-

likely to be successful unless (1) the environment is changed to ameliorate the limiting factors or (2) biotic agents adapted to the modified environment are discovered or developed.

Opportunistic pests are characterized by extraordinarily wide-amplitude population fluctuations wherever conditions of food and weather are favorable. Their great reproductive potential and great powers of dispersal resemble those of the opportunistic species described by Cole (1966): "plants and animals that are normally inconspicuous but that quickly invade and occupy a temporary habitat." These pests may be attacked by a large complex of biotic agents, but are regarded as being largely under the influence of density-independent rather than density-dependent factors (Watt 1968).

The lack of sources of new biotic agents attacking pests of this type has discouraged the biological control approach, and the few attempts made have failed (i.e., the spruce budworm; *Miller and Angus, in press*). Although these species are frequently abundant over wide areas in their native lands, it is remarkable that few of them have become pests in other continents. This apparent inability to colonize new areas may be related to the importance of density-independent factors in their life systems. The same non-governing factors that determine generation survival in the native land are likely to be present and of similar importance in the new environment. The chance of such a species becoming established in a new region might therefore only be high during the relatively brief periods when these factors are favourable. On the other hand, species whose fluctuations are determined by biotic governing factors, except competition for food, escape these governing influences in a new environment and commonly find combinations of density-independent factors that are suitable for both establishment and rapid increase.

Thus a species exhibiting low-amplitude population fluctuations in its native home would probably be characterized by wide-amplitude fluctuations in a new environment, possibly exceeding those characteristic of native opportunistic pests. Such species in a new environment may continue to increase until the food supply is almost totally destroyed, thus leading to their

own extinction in localized areas and marked instability of the ecosystem of which they form a part.

Low-density pests present a difficult problem for biological control. They do not exhibit wide-amplitude population fluctuations and are usually considered to be well governed. Since effective density-dependent agents are already present, there is not much scope for classical biological-control approaches. This category includes many of the species called "direct pests" by Turnbull and Chant (1961) but excludes those direct pests that attain high densities. Although classification on the basis of direct or indirect damage is useful for emphasizing the degree of population reduction necessary for economic control, classification on the basis of the population dynamics of the pest gives a more realistic evaluation of the best strategy for an integrated control program. For example, *Adelges piceae* is a species that is classified as a "direct pest" by Turnbull and Chant (1961). We would classify it as typically anthropogenic in Europe, where it is endemic on the older trees of the common silver fir *Abies alba* in mature stands but often a pest in the mixed age plantings that have been made outside the natural range (Pschorn-Walcher 1964), and as typically exotic in America.

The development of integrated control strategies must be based on both the population characteristics of the pest and the various types of control operation that are available. Past experience, theory, and investigation of specific situations should dictate the most promising integrated control approach. A large proportion of past biological-control programs have utilized parasites; and this experience, plus the theory developed from population-dynamics studies, provides a basis for utilizing parasites in integrated control programs.

Analysis of Programs Against Forest Insects

The history of biological-control attempts against forest insects in North America has been reviewed by Dowden (1962) and McGugan and Coppel (1962). They list 44 target species for programs in which parasites were used; and we added a 45th species, the holly leaf miner, following Turnbull and Chant

(1961). Since the period covered by these reviews, a few new programs involving parasites have been initiated: against the larch sawfly, the European pine shoot moth, the European pine sawfly, and the winter moth in Canada; and against the European elm bark beetle, the larch casebearer, and the western spruce budworm in the U.S.A.

The record of parasite releases against forest pests is rather blurred and confused in places. In attempting to evaluate this record, we have been forced to make decisions regarding the various programs on the basis of incomplete data. The results may be biased, but, if we are to advocate the use of parasites in integrated control programs, we must be prepared to give some estimate of the chances of success.

On the basis of published information, each target species was classified as to pest type (exotic, anthropogenic, opportunistic, low-density) and whether it was a "prime" or "alternative" target for parasite releases: prime targets are known to be hosts of the parasite species released against them; alternative targets are those against which parasites from related host species were released on the basis of a reasonable chance of success or merely to dispose of surplus material. In this empirical evaluation it was necessary to exclude a large number of the programs listed because: release and recovery data were inadequate; the parasite was probably already present; only a single release of the parasite was made; the parasite was introduced to Canada from a subtropical source; the parasites released were obtained from host species distantly related and ecologically dissimilar from the target species.

Most of the 21 programs that were considered amenable to analysis, and most of the successful programs, were against exotic pests (table 1). Only three attempts were made against anthropogenic and two against opportunistic pests. Among these five, the single successful biological control attempt was against an anthropogenic pest, the pine tip moth, and in this case the pest situation had many resemblances to that of an exotic pest: serious damage to pine plantations was being caused by *Rhyacionia frustrana bushnelli* in Nebraska where effective parasites were absent; while *R. frustrana frustrana* in Virginia was effec-

Table 1—Target Species for Major Biological Control Programs
Using Parasites Against Forest Insects in North America

Species	Origin	Type ¹	Results ²
HOMOPTERA			
<i>Lecanium tiliae</i> L.—lecanium scale	Exotic	Prime	C
<i>Gossyparia spuria</i> (Mod.)—European elm scale	"	"	S
COLEOPTERA			
<i>Galerucella xanthomelaena</i> (Schr.)—elm leaf beetle	"	"	C
DIPTERA			
<i>Phytomyza ilicis</i> (Curt.)—Holly leaf miner	"	"	C
LEPIDOPTERA			
<i>Choristoneura fumiferana</i> (Clem.)—spruce budworm	Native	"	U
<i>Cnidocampa flavescens</i> (Wlkr.)—oriental moth	Exotic	"	C
<i>Coleophora laricella</i> (Hbn.)—larch casebearer	"	"	S
<i>Hemerocampa leucostigma</i> (J. E. Smith)—white-marked tussock moth	Native	Alternative	U
<i>Lambdina fiscellaria</i> (Guen.)—eastern hemlock looper	"	Prime	U
<i>Operophtera brumata</i> (L.)—winter moth	Exotic	"	S
<i>Porthetria dispar</i> (L.)—gypsy moth	"	"	C
<i>Nygmia phaerrhoea</i> (Donov.)—brown-tail moth	"	"	C
<i>Rhyacionia frustrana bushnelli</i> (Busck)—pine tip moth	Native	"	S
<i>Rhyacionia buoliana</i> (Schiff.)—European pine shoot moth	Exotic	Prime	U
<i>Stilpnotia salicis</i> (L.)—satin moth	"	"	C
HYMENOPTERA			
<i>Diprion hercyniae</i> (Htg.)—European spruce sawfly	"	"	S
<i>Diprion similis</i> (Htg.)—introduced pine sawfly	"	"	S
<i>Heterarthrus nemoratus</i> (Fall.)—birch leaf-mining sawfly	"	"	C

<i>Neodiprion lecontei</i> (Fitch)—red-headed pine sawfly	Native	Alternative	U
<i>Neodiprion sertifer</i> (Geoff.)—European pine sawfly	Exotic	Prime	U
<i>Pristiphora erichsonii</i> (Htg.)—larch sawfly	" 3	"	C

¹See text for definitions.

²U = Unsuccessful, C = Contributive, S = Successful—See text for definitions.

³Origin disputed but here listed as "Exotic" because of its poor complex of parasites in North America (*Pschorn-Walcher* 1963).

tively controlled by parasites (*Dowden* 1962). The distribution of the two subspecies was disjunct, and thus this example cannot be used to predict the results of parasite releases against anthropogenic pests.

Consideration of the results of parasite releases against native (anthropogenic plus opportunistic) and exotic pests suggests that prospects for manipulating pest populations with pest releases are quite good (table 2). At least one new parasite was established on all the exotic species and on 40 percent of the native target species. The lesser success of releases against native target species may be taken to indicate that these pests are less suitable to the establishment of new parasites, but the record also suggests that the effort applied to these programs has been less than for introduced pests: the average number of parasite species released per native pest is 7.8; per exotic pest it is 9.4.

The results indicate that the prospect for quantitatively increasing the parasite complex is high for exotic pests and reasonably good for native pests. The fortuitous establishment of parasites released against the gypsy and browntail moths, the European spruce sawfly, and the European pine sawfly also shows that the parasite complex of native species can be increased by introductions.

The rate of successful establishment in relation to the total number of parasite species released was approximately one-third (table 2). This is undoubtedly a gross underestimate of the probability that an introduced species can be established, because in many programs difficulties with handling, synchroniza-

Table 2.—Results of Biological Control Programs Using Parasites
Against Forest Insects in North America

Origin of target species	Type of program ¹	Number of species		Establishment (%)—		Control ¹ (% of target species)			Excluded species
		Target	Parasites released	on target spp. ²	of parasite spp. ³	C	S	C + S	
		<i>No.</i>	<i>No.</i>	<i>Pct.</i>	<i>Pct.</i>	<i>Pct.</i>	<i>Pct.</i>	<i>Pct.</i>	<i>No.</i>
Native	Prime	3	28	33	4	0	33	33	2
	Alternative	2	11	50	18	0	0	0	17
Exotic	Prime	16	151	100	37	56	31	88	2
	Alternative	0							3
All species	—	21	190	90	32	43	29	71	24

¹See text for definitions.

²Target species on which at least one new parasite was established/total target species.

³Number of parasite species established/total number of species released.

tion, and small numbers of parasites available, mitigated against success. In our own experience, the failure of four of the six species of parasites released against the larch sawfly since 1961 can be attributed mainly to our lack of knowledge of conditions necessary to ensure mating and maintain vigor of parasite adults between emergence and release (*Turnock and Muldrew, in press*).

Evaluation of the effect of the introduction of a parasite on the target species should be based not only on its contribution to a reduction in pest population levels, but also to the reduction in damage to trees. Unfortunately, such information is rarely collected, and for many programs even crude data on the level of parasitism in the population is available for only a few years following the release. We therefore evaluate the biological-control programs on the basis of three categories:

1. *Successful*: populations and damage reduced to acceptable levels.
2. *Contributive*: introduced parasites causing appreciable mortality and believed to be contributing to the reduction of the intensity, duration, or frequency of outbreaks of the target species.
3. *Unsuccessful*: released parasites either not recovered, or occurring sporadically or at very low numbers.

Successful control was attained against 31 percent of the exotic and 33 percent of the native pests that were prime targets for parasite introduction. Contributive control was attained against 56 percent of the exotics but none of the native pests. The latter group comprises too small a number of species to allow the conclusion that parasite introductions are unlikely to contribute to the control of native pests.

Evaluation of Past Programs

Parasite release has been shown to have had some controlling effect on pest populations in a remarkably high proportion of the attempts, even though cases have been included where the

knowledge and resources applied to the program were minimal. The failure to adequately support biological-control programs can in part be attributed to the prevalence of too casual an attitude to the problems of parasite establishment. Although we eliminated from consideration many ill-conceived or poorly executed programs, the remainder still includes cases where parasites were released in poor condition, in poor synchronization with the preferred host stage, unmated, in inadequate numbers, or in suboptimal environments.

The problems of past programs can be attributed basically to a lack of proper standards in scientific procedure. Too often, little attention has been paid to researching the problems, to selecting appropriate biotic agents, to ensuring proper care of these agents before release, to selecting optimum release areas, and to assessing the host-density determinants before and after the initiation of the program. Reasons for this have been that many programs were conducted by forest entomologists lacking an adequate background in population dynamics and biological control and that financial support has been inadequate. Past expenditures on biological control have been small in relation to both the benefits achieved and the expenditures made on chemical control. The favorable cost-benefit ratio of biological control would be even more impressive if the costs due to undesirable side-effects of chemical control and possible future detoxification of polluted environments could be included. At present there is too little appreciation of the relatively low cost and lasting benefits of biological control. Since there is slight incentive for industry to develop biological control, public bodies must accept the responsibility for encouraging and supporting this type of program.

Recommendations for Parasite Use in Integrated Control

Integrated control for forest pests is applied population dynamics (*Balch 1964*). Continued maintenance of pest numbers below the economic threshold for damage must be based on knowledge of pest ecology and damage thresholds. In selecting

control methods for use in integrated programs, an attempt should be made to forecast the effects of specific actions on other mortality factors and short- and long-term population trends. In the absence of good models for predicting population trends, integrated control planning should initially concentrate on the evaluation of existing natural control. In analyses of the target species, the efficiency of natural and applied control factors and their inter-actions must be examined for different stages of the insect and for different ecological situations in which the pest occurs.

The concept of "guilds" of biological agents attacking a pest appears to be a very useful tool in planning integrated control. Root (1967) defines a guild as "a group of species that exploit the same class of environmental resources in the same way. This term groups together species, without regard to taxonomic position, that overlap significantly in their niche requirements." This can be considered as an expansion of the concept of "parasitological niches" defined by Zwolfer (1961) in the following way: "... holometabolic insects (possess) several biologically and ecologically differentiated stages, which are attacked by a number of different types of parasites. Host species such as these offer to entomophagous insects a system of diversified opportunities for oviposition and larval development, providing what, in analogy with the ecological niches of the habitat, may be considered as a complex of parasitological niches."

Although this concept is useful in investigating the parasite complex of pest species to reveal niches where the parasite complex is deficient in species or in effectiveness, the "guild" concept has a wider application. The target species can be considered as offering a complex of niches, which are exploited, to a greater or lesser degree, by the various guilds of biological agents. These guilds may attack different life stages of the pest, or individuals that occur in particular parts of trees, stand types, or site conditions. For example, for certain pests it may be sufficient to determine that the guild of larval parasites, predators, and diseases is lacking in species and effectiveness, while for other species the larval guild may be efficient in some stands and climatic zones but not in others. Thus in west-

ern larch stands the larch sawfly larval parasite guild appears reasonably effective (*Molnar et al. 1966*) while the same guild is ineffective in continental stands of tamarack, apparently because the "resistant" strain of larch sawfly is present (*Muldrew 1953*), as well as in tamarack stands of Newfoundland, possibly because of unfavorable climatic conditions. The approaches to integrated control in these three situations would be quite different.

Utilization of parasites in control operations can involve various methods of releasing parasites, of enhancing parasite efficiency by manipulating other aspects of the environment, and of using parasites to improve other mortality factors. Most parasite releases against forest insects have been of the *colonization* type: a relatively small colony of a new parasite species is established in a region where it is expected to become a permanent part of the natural control complex.

Inoculative releases are periodic releases in which control is dependent upon progeny being produced for more than one generation following colonization. They are usually made to establish an enemy in areas from which it is temporarily absent due to adverse environmental conditions, and they have been used against agricultural and horticultural pests (*DeBach and Hagen 1964*), but not in forestry. Integrated control of pests of trees at the periphery of the range of effective parasite species might well involve such inoculative releases. In addition, inoculative releases early in the development of an outbreak could be used to speed parasite response to pest population increases.

Inundative releases are also periodic, but are made to control a pest by the actions of the natural enemies released, not by their progeny. Their potential has not received much attention in forest entomology, but they might be used to advantage in relatively small areas where chemical insecticides are undesirable but which are not suitable for the application of pathogenic insecticides: e.g., where the terrain, tree size, or stand density are unsuitable for the spray equipment. The application of this technique depends on the availability of large numbers of parasites at low cost. The egg parasite *Trichogramma* has

been used in this way against agricultural pests, and tests against the spruce budworm in western North America are now planned. Larval and cocoon parasites offer some promise for use in inundative releases in incipient outbreaks where damage caused by the target generation of the pest can be tolerated.

The enhancement of parasite effectiveness through environmental manipulation to eliminate or ameliorate conditions detrimental to the maximum expression of control potential of parasite species must play an important part in pest management. As a first step, the effects of poor timing or unnecessarily high kills associated with insecticidal control must be minimized. Integrated control will not progress far until the use of applications of chemical and biological insecticides at dosages causing nearly 100 percent mortality is confined to situations where such applications are essential: i.e., small areas of high-value crop with low damage thresholds and situations where eradication is possible. Insecticidal applications should be aimed at achieving the minimum mortality compatible with crop protection.

Information on the critical factors influencing the abundance of parasites and their ability to control their hosts is sadly lacking. The widely accepted idea that host abundance is usually the major factor controlling parasite abundance appears logically untenable in the light of studies of phytophagous species. Since many of the latter are prevented by other factors from fully exploiting their food source, we should expect a similar situation to exist for many parasite species. Studies of the population dynamics of parasitic species are badly needed to elucidate their controlling mechanisms.

The presence of special habitats, other than those occupied by their host, may be necessary for the survival of some parasite species. Flowering plants may be used as feeding sites for some species; e.g. two parasites of the European pine shoot moth leave the pines to dwell among the flowers of Umbelliferae (*Thorpe and Caudle 1938*), and the preoviposition period of female *Eucarcelia rutilla* is spent in oak rather than pine woods inhabited by its host (*Herrebout 1967*). The absence of

alternate hosts may limit the efficiency of some polyphagous parasites, particularly where a univoltine host is attacked by a bivoltine parasite. Increased parasite effectiveness might be attained by providing suitable alternate hosts, perhaps by encouraging plant species on which they feed. Other possibly limiting aspects of the environment which might be manipulated by management techniques are: shelter for overwintering parasite adults; protection from biotic enemies (e.g., ants), and improvement of the physical environment through the encouragement of specific plant growth for shelter.

Another opportunity for improving the efficiency of parasites lies in the selection of superior genetic strains for release against the target pest. This approach has been used in Manitoba against the larch sawfly. Muldrew (1953) showed that the larch sawfly in Manitoba was capable of encapsulating and killing the eggs of *Mesoleius tenthredinis*. This resistant strain has since spread until it now occurs from northeastern British Columbia to Nova Scotia. Experimental testing of *M. tenthredinis* from Europe and Japan revealed that the *M. tenthredinis* from Bavaria was capable of overcoming the encapsulation reaction of "resistant" larch sawflies and that this ability was inherited by the progeny of Canadian and Bavarian crosses. In 1963 and 1964, releases of Bavarian *M. tenthredinis* were made at two locations in Manitoba, and the encouraging results to date suggest the *M. tenthredinis* may again contribute to the control of the larch sawfly (Turnock and Muldrew, *in press*).

Selection of parasite strains also may be useful where bivoltine parasites attack univoltine hosts. If suitable alternate hosts are not available, relocation or development of a univoltine strain may be possible. We also can contemplate the use of secondary and tertiary parasites to improve the effectiveness of an existing parasite complex. Secondaries might be used to reduce the competitive stress of an ineffective primary on a potentially effective one. Tertiary parasites might reduce the deleterious effects of a secondary parasite on a primary.

The opportunity to use parasites to actively enhance the effectiveness of other control measures would appear to be limited, at present, to the introduction of a parasite species capable

of acting as a vector for an effective pathogen. Such a relationship now exists between the effective introduced parasites and the virus disease of the European spruce sawfly in eastern North America (Neilson *et al.*, *in press*). The virus introduced against the European pine sawfly lacks an effective dispersing agent and is at present effective only as an insecticidal spray (Griffiths *et al.*, *in press*). The selection and introduction of a parasite with the ability to disseminate this virus might improve the level of total control.

The integrated control approach to the management of a particular pest species may include active measures to increase the efficacy of enemies through release and enhancement programs or may merely avoid the use of other controls that decrease efficacy. In either case, no intelligent strategy can be developed without knowledge of the composition and effectiveness of the enemies in various guilds. The selection of parasites for release programs should be based on the comparison of guilds in the donor and recipient areas while enhancement programs would benefit from comparative studies of guilds in different stands and climates.

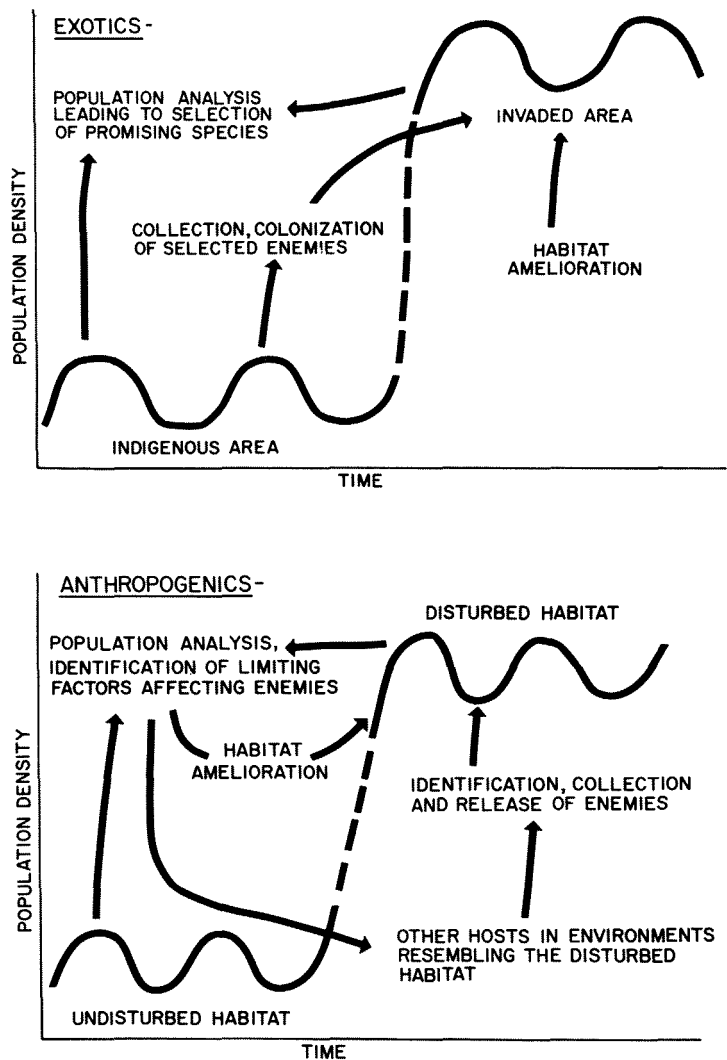
The place of parasites in integrated control operations would appear to vary with the type of pest. We would stress the importance of population analysis leading to the identification of ineffective guilds as a first step in planning the integrated control of any type of pest (fig. 1).

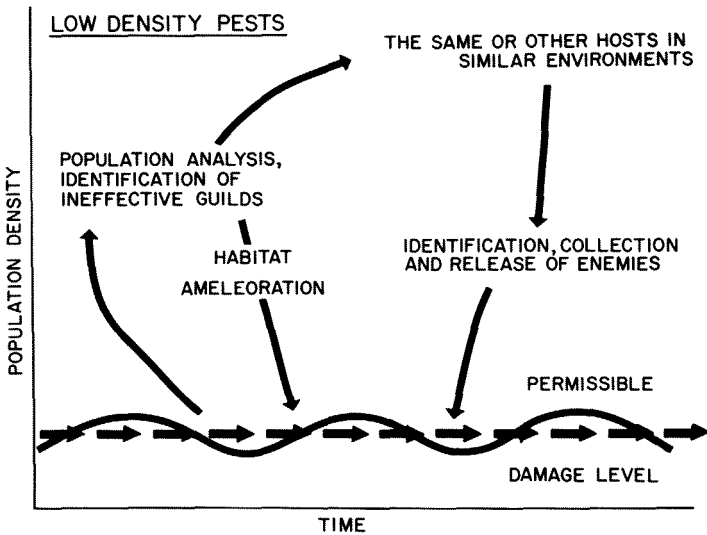
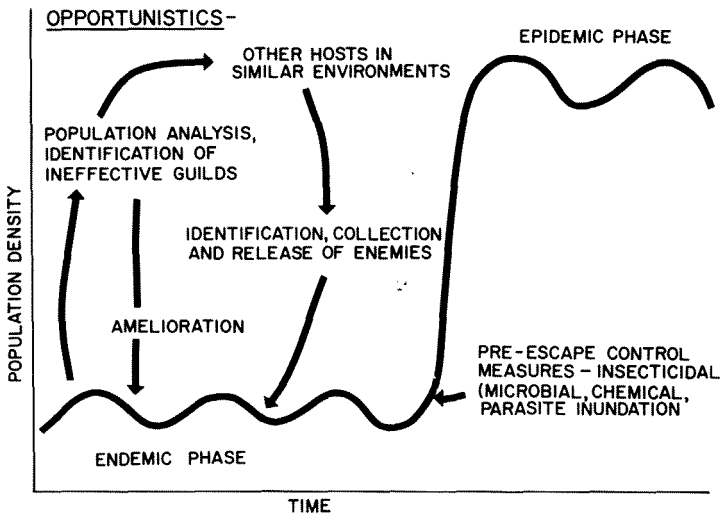
The identification and release of promising parasite species for colonization releases appears to be the most useful approach to the integrated control of exotic pests (fig. 1A). Insecticidal practices that would obstruct parasite establishment or effectiveness should be avoided. If habitat conditions in the invaded area appear suboptimal for otherwise preferred parasite species, habitat amelioration may also be considered.

Although not all exotic pests are under effective economic control throughout their indigenous area, effective parasites may still be found for colonization releases. For example, the larch sawfly is anthropogenic in Europe while in North America it is a pest of undisturbed forests. Material for the recent release of the apparently effective parasite, *Olesicampe benefac-*

tor, was obtained in Europe from larch plantations where the larch sawfly was abundant as well as from native stands where it was consistently uncommon. Exotics that are opportunistic pests in their indigenous area may also offer an opportunity for

Figure 1.—Suggested strategy for biological and integrated control in relation to the population dynamics of four types of pests.





colonization of parasites. Here the basic assumption is that there are factors in the native home of the pest that inhibit parasite efficacy and that these inhibitors need not occur in the invaded area. Such factors may include hyperparasites, cleptoparasites (*Spradbery 1969*), predators, diseases, and competitors. In addition, differences between host trees and conditions of the physical environment in the new habitat as compared to

the native one may enhance the activity of certain parasite species.

With anthropogenic pests the main initial effort should be directed towards determining the reasons for the presence of control in natural habitats and the lack of it in modified habitats (fig. 1B). From this analysis the treatment required for rectification in the disturbed habitats may be evident. Such treatment may involve a cultural or stand-management approach or an attempt to enhance the effects of those biotic agents of control already present. It may involve a search in foreign areas for preadapted parasites of taxonomically or ecologically related hosts. Insecticidal applications will probably be necessary, but efforts should be made to ensure that the dosage and timing used are related to maximizing total control.

With opportunistic pests (fig. 1C), the initial effort should probably be on studies to determine whether the existing biotic factors, particularly those that act at endemic levels, can be enhanced. If this approach fails, a search in foreign lands for parasites of taxonomically or ecologically related species should be made. The possibility of forcing a change in the host preference of a parasite species that is not indigenous to the invaded area by cage parasitization and laboratory rearings should not be overlooked. The application of insecticides (chemical, microbial, inundative releases) during early phases of population build-up to prevent climatic release of the pest should be tested.

Since low-density pests are characterized by low-amplitude population fluctuations, (fig. 1D), improvement of the natural control complex may prove difficult. Colonization of new parasite species from other areas and enhancement of existing parasite efficacy may be possible, but the necessity for periodic control operations will probably remain. As an alternative to chemical and microbial insecticides, inundative releases of native parasites might be useful to avoid environmental contamination and application problems associated with biocides. In some cases, the most valid approach would be to promote public acceptance of a somewhat higher level of damage.

In conclusion, we would emphasize that although there has been considerable talk about the applicability of integrated con-

trol approaches to forest pest management, few attempts have been made. This approach has been successfully used against agricultural pests (see Bartlett 1964; van den Bosch and Stern 1962) particularly in orchards where conditions are similar to the forest ecosystem. Beirne (1962) suggested that neglect of the integrated approach was due to the amount and complexity of background information that must be gathered before the method becomes operational, the reluctance of growers to reduce applications of chemicals (or to suffer some damage while giving biotic agents a fair chance to build up), and the inability of proponents of opposite schools of thought to cooperate. We might also add that another contributing factor to this neglect may be that the method is still in its infancy and the knowledge and techniques necessary to enable its growth into vigorous adulthood still await discovery and development.

References

- Andrewartha, H. G., and L. C. Birch
1954. THE DISTRIBUTION AND ABUNDANCE OF ANIMALS. 782 pp. Univ. Chicago Press, Chicago.
- Auer, C.
1969. A SIMPLE MATHEMATICAL MODEL FOR "KEY-FACTOR" ANALYSIS AND COMPARISON. Swiss Federal Inst: Tech., Zurich. The working group on the population dynamics of *Zeiraphera diniana*. Commun. 34: 8 pp.
- Balch, R. E.
1964. THE FUTURE IN FOREST ENTOMOLOGY. J. Forestry 62: 11-18.
- Bartlett, B. R.
1964. INTEGRATION OF CHEMICAL AND BIOLOGICAL CONTROL. IN BIOLOGICAL CONTROL OF INSECT PESTS AND WEEDS. Ed. P. DeBach. pp. 489-511. Reinhold Publishing Corp., New York.
- Beirne, B. P.
1962. TRENDS IN APPLIED BIOLOGICAL CONTROL OF INSECTS. Ann. Rev. Entomol. 7: 387-400.
- Buckner, C. H.
1966. THE ROLE OF VERTEBRATE PREDATORS IN THE BIOLOGICAL CONTROL OF FOREST INSECTS. Ann. Rev. Entomol. 11: 449-470.
- Buckner, C. H., and W. J. Turnock
1965. AVIAN PREDATION ON THE LARCH SAWFLY, *PRISTIPHORA ERICHSONII* (HTG.) (HYMENOPTERA: TENTHREDINIDAE). Ecol. 46: 223-236.
- Clausen, C. P.
1956. BIOLOGICAL CONTROL OF INSECT PESTS IN THE CONTINENTAL UNITED STATES. USDA Tech. Bull. 1139, 151 pp.
- Cole, L. C.
1966. THE COMPLEXITY OF PEST CONTROL IN THE ENVIRONMENT. IN SCIENTIFIC ASPECTS OF PEST CONTROL. Nat. Acad. Sci. Pub. 1402: 13-25. Washington, D.C.
- DeBach, P.
1964. SUCCESSES, TRENDS, AND FUTURE POSSIBILITIES. IN BIOLOGICAL CONTROL OF INSECT PESTS AND WEEDS. Ed. P. DeBach. pp. 673-713. Reinhold Publishing Corp., New York.
- DeBach, P. and K. S. Hagen
1964. MANIPULATION OF ENTOMOPHAGOUS SPECIES. IN BIOLOGICAL CONTROL OF INSECT PESTS AND WEEDS. Ed. P. DeBach. pp. 429-458. Reinhold Publishing Corp., New York.
- Doutt, R. L. and P. DeBach
1964. SOME BIOLOGICAL CONTROL CONCEPTS AND QUESTIONS. IN BIOLOGICAL CONTROL OF INSECT PESTS AND WEEDS. Ed. P. DeBach. pp. 118-

142. Reinhold Publishing Corp., New York.
- Dowden, P. B.
1962. PARASITES AND PREDATORS OF FOREST INSECTS LIBERATED IN THE UNITED STATES THROUGH 1960. USDA Agr. Handbook 226, 70 pp.
- Embree, D. G.
1965. THE POPULATION DYNAMICS OF THE WINTER MOTH IN NOVA SCOTIA: 1954-1962. Entomol. Soc. Can. Mem. 46, 57 pp.
- Griffiths, K. J., A. H. Rose and F. T. Bird
[In Press.] NEODIPRION SERTIFER (GEOFF.), EUROPEAN PINE SAWFLY (HYMENOPTERA: DIPRIONIDAE). IN BIOLOGICAL CONTROL PROGRAMS AGAINST INSECTS AND WEEDS IN CANADA, 1959-1968.
- Herrebout, W. M.
1967. HABITAT SELECTION IN EUCARCELIA RUTILLA VILL. (DIPTERA: TACHINIDAE). I OBSERVATIONS ON THE OCCURRENCE DURING THE SEASON. Zeit. f. ang. Entomol. 60: 219-229.
- Huffaker, C. B. and C. E. Kennett
1969. SOME ASPECTS OF ASSESSING EFFICIENCY OF NATURAL ENEMIES. Can. Entomol. 101: 425-447.
- Huffaker, C. B. and P. S. Messenger
1964. THE CONCEPT AND SIGNIFICANCE OF NATURAL CONTROL. IN BIOLOGICAL CONTROL OF INSECT PESTS AND WEEDS. Ed. P. DeBach. pp. 74-117. Reinhold Publishing Corp., New York.
- Ives, W. G. H., W. J. Turnock, C. H. Buckner, R. J. Heron and J. A. Muldrew
1968. LARCH SAWFLY POPULATION DYNAMICS: TECHNIQUES. Manitoba Entomol. 2: 5-36.
- Klomp, H.
1966. THE DYNAMICS OF A FIELD POPULATION OF THE PINE LOOPER, BUPALUS PINIARIUS L. (LEP., GEOM.) Adv. Ecol. Res. 3: 207-305.
- Liu, Chung-lo
1958. MONOPHAGY VERSUS POLYPHAGY IN THE CHOICE OF ENTOMOPHAGOUS INSECTS IN BIOLOGICAL CONTROL. Int. Conf. Insect Pathol. Biol. Control, 1st. Trans. 1958: 521-531. Prague.
- Mattson, W. J., F. B. Knight, D. C. Allen, and J. L. Foltz
1968. VERTEBRATE PREDATION ON THE JACK PINE BUDWORM IN MICHIGAN. J. Econ. Entomol. 61: 229-234.
- McGugan, B. M. and H. C. Coppel
1962. A REVIEW OF THE BIOLOGICAL CONTROL ATTEMPTS AGAINST INSECTS AND WEEDS IN CANADA. PART II. BIOLOGICAL CONTROL OF FOREST INSECTS, 1910-1958. Tech. Commun. 2, 35-216, C.I.B.C., Trinidad.
- Miller, C. A.
1963. PARASITES AND THE SPRUCE BUDWORM. IN THE DYNAMICS OF EPIDEMIC SPRUCE BUDWORM POPULATIONS. Ed. R. F. Morris. Entomol. Soc. Can. Mem. 31: 228-244.
- Miller, C. A.
1966. THE BLACK-HEADED BUDWORM IN EASTERN CANADA. Can. Entomol. 98: 592-613.
- Miller, C. A. and T. A. Angus
[In Press.] CHORISTONEURA FUMIFERANA (CLEMENS), SPRUCE BUDWORM (LEPIDOPTERA: TORTRICIDAE). IN BIOLOGICAL CONTROL PROGRAMS AGAINST INSECTS AND WEEDS IN CANADA, 1959-1968.
- Molnar, A. C., J. W. E. Harris and D. A. Ross
1966. BRITISH COLUMBIA REGION. IN REPORT OF THE FOREST INSECT AND DISEASE SURVEY. Can. Dep. Forestry and Rural Develop., Forestry Br. 108-123.
- Morris, R. F.
1959. SINGLE-FACTOR ANALYSIS IN POPULATION DYNAMICS. Ecol. 40: 580-588.
- Morris, R. F., ed.
1963. THE DYNAMICS OF EPIDEMIC SPRUCE BUDWORM POPULATIONS. Entomol. Soc. Can. Mem. 31, 332 pp.
- Morris, R. F.
1969. APPROACHES TO THE STUDY OF POPULATION DYNAMICS. IN FOREST INSECT POPULATION DYNAMICS. USDA Forest Serv. Res. Paper NE-125: 9-28, illus. NE. Forest Exp. Sta. Upper Darby, Pa.
- Muldrew, J. A.
1953. THE NATURAL IMMUNITY OF THE LARCH SAWFLY, (PRISTIPHORA ERICHSONII (HTG.)) TO THE INTRODUCED PARASITE MESOLEIUS TENTHREDINIS MORLEY, IN MANITOBA AND SASKATCHEWAN. Can. J. Zool. 31: 313-332.
- National Academy of Sciences.
1969. PRINCIPLES OF PLANT AND ANIMAL PEST CONTROL VOL. 3 INSECT-

- PEST MANAGEMENT AND CONTROL. Nat. Acad. Sci. Pub. 1695. 508 pp. Washington, D.C.
- Neilson, M. M., R. Martineau and A. H. Rose
[In Press.] DIPRION HERCYNIAE (HTG.) EUROPEAN SPRUCE SAWFLY (HYMENOPTERA: DIPRIONIDAE). IN BIOLOGICAL CONTROL PROGRAMS AGAINST INSECTS AND WEEDS IN CANADA, 1959-1968.
- Nicholson, A. J.
1954. AN OUTLINE OF THE DYNAMICS OF ANIMAL POPULATION. Aust. J. Zool. 2: 9-65.
- Nicholson, A. J. and V. A. Bailey
1935. THE BALANCE OF ANIMAL POPULATIONS. Zool. Soc. London Proc. Part I: 551-598.
- Prebble, M. L.
1960. BIOLOGICAL CONTROL IN FOREST ENTOMOLOGY. Entomol. Soc. Amer. Bull. 6: 6-8.
- Pschorn-Walcher, H.
1963. HISTORISCH-BIOGEOGRAPHISCHE RUCKSCHLUSSE AUS WIRT-PARASITEN-ASSOCIATIONEN REI INSEKTEN. Zeit. f. ang. Entomol. 51: 208-214.
- Pschorn-Walcher, H.
1964. COMPARISON OF SOME DREYFUSIA (=ADELGES) INFESTATIONS IN EURASIA AND NORTH AMERICA. Commonwealth Inst. Biol. Contr. Tech. Bull. 4: 1-23.
- Pschorn-Walcher, H. D. Schroder and O. Eichhorn
1969. RECENT ATTEMPTS AT BIOLOGICAL CONTROL OF SOME CANADIAN FOREST INSECT PESTS. Commonwealth Inst. Biol. Contr. Tech. Bull. 11: 1-18.
- Root, R. B.
1967. THE NICHE EXPLOITATION PATTERN OF THE BLUE-GRAY GNAT-CATCHER. Ecol. Monogr. 37:317-350.
- Simmonds, F. J.
1956. THE PRESENT STATUS OF BIOLOGICAL CONTROL. Can. Entomol. 88: 553-563.
- Spradbery, J. P.
1969. THE BIOLOGY OF PSEUDORHYSA STERNATA MERRILL (HYM., ICHNEUMONIDAE), A CLEPTOPARASITE OF SIRICID WOODWASPS. Ent. Res. Bull. 59: 291-297.
- Stark, R. W.
1959. POPULATION DYNAMICS OF THE LODGEPOLE NEEDLE MINER, RECURVARIA STARKI FREEMAN, IN CANADIAN ROCKY MOUNTAIN PARKS. Can. J. Zool. 37: 917-943.
- Syme, P. D.
[In Press.] RHYACIONIA BUOLIANA (SCHIFF.), EUROPEAN PINE SHOOT MOTH (LEPIDOPTERA: OLETHREUTIDAE). In Biol. Contr. against Insects and Weeds in Canada, 1959-1968.
- Taylor, T. H. L.
1955. BIOLOGICAL CONTROL OF INSECT PESTS. Ann. Appl. Biol. 42: 190-196.
- Thorpe, W. H., and H. B. Caudle
1938. A STUDY OF THE OLFACTORY RESPONSES OF INSECT PARASITES TO THE FOOD PLANT OF THEIR HOST. Parasitology 30: 523-528.
- Turnbull, A. L. and D. A. Chant
1961. THE PRACTICE AND THEORY OF BIOLOGICAL CONTROL OF INSECTS IN CANADA. Can. J. Zool. 39: 697-753.
- Turnock, W. J.
1969. PREDATION BY LARVAL ELATERIDAE ON PUPAE OF THE PINE LOOPER, BUPALUS PINIARIUS (L). Netherlands J. Zool. 19: 393-416.
- Turnock, W. J. and J. A. Muldrew
[In Press.] PRISTIPHORA ERICHSONII (HTG.), LARCH SAWFLY. (HYMENOPTERA: TENTHREDINIDAE). In Biol. Contr. Programs against Insects and Weeds in Canada, 1959-1968.
- van den Bosch, R. and V. M. Stern
1962. THE INTEGRATION OF CHEMICAL AND BIOLOGICAL CONTROL OF ARTHROPOD PESTS. Ann. Rev. Entomol. 7: 367-386.
- Varley, G. C. and G. R. Gradwell
1970. RECENT ADVANCES IN INSECT POPULATION DYNAMICS. Ann. Rev. Entomol. 15: 1-24.
- Watt, K. E. F.
1968. ECOLOGY AND RESOURCE MANAGEMENT. 450 pp. McGraw-Hill Book Co., New York.
- Wolcott, G. W.
1958. THE EVANESCENCE OF PERFECT BIOLOGICAL CONTROL. 10th Int. Congr. Entomol. 1956 Proc. 4: 511-513. Montreal.
- Zwölfer, H.
1961. A COMPARATIVE ANALYSIS OF THE PARASITE COMPLEXES OF THE EUROPEAN FIR BUDWORM, CHORISTONEURA MURINANA (HUB.) AND THE NORTH AMERICAN SPRUCE BUDWORM, C. FUMIFERANA (CLEM.). Commonwealth Inst. Biol. Control. Tech. Bull. 1: 1-162.