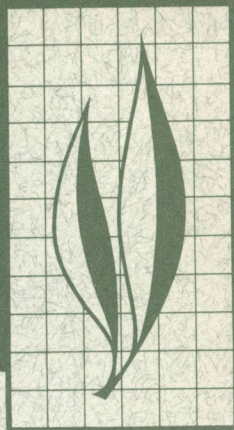


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Mechanisms of Population Homeostasis in *Anagasta* Ecosystems

S. E. Flanders

UNIVERSITY OF CALIFORNIA DIVISION OF AGRICULTURAL SCIENCES



This reports on continuing investigations of prey-predator interactions in long-lived ecosystems comprising self-perpetuating populations of the moth *Anagasta kuebniella* (Zeller) and its pathogen, the larva-infecting *Bacillus thuringiensis* Berliner; its predator, the egg-feeding mite *Blattisocius tarsalis* (Berlese); and its endoparasite, the larva-feeding wasp *Devorgilla canescens* (Gravenhorst). Invasions by a predator, the flour beetle *Tribolium confusum* Jacquelin duVal, are analyzed. These *Anagasta* ecosystems demonstrate the basic regulatory mechanisms of any self-perpetuating population wherever located. These ecosystems have demonstrated that the maintenance of balance between a host and its parasite is either nonreciprocal or reciprocal, a differentiation that is determined by the degree to which the host is *fortuitously* protected from parasitization. When a natural enemy population is in reciprocal balance with that of its prey, regulating the population density of both its prey and itself, the food supply of the prey automatically becomes for the prey an unlimited resource. This occurs in the *Anagasta* ecosystems despite the fact that the strictly limited amount of food is replaced, whether wholly used or not, according to certain schedules. As in nature the abundance of an established animal population (the relative numbers of individuals in an area) is an expression of (1) the distribution of favorable habitats (disposition of individuals or groups over an area), and (2) the population saturation levels of such habitats (the full occupancy of a locality as determined by environmental resistance to population reproductivity).

THE AUTHOR:

S. E. Flanders is Emeritus Professor of Biological Control and Emeritus Entomologist in the Citrus Research and Agricultural Experiment Station, Riverside.

Mechanisms of Population Homeostasis in *Anagasta* Ecosystems¹

INTRODUCTION

CROP CONSERVATION through biological control approaches its maximum when the prevailing equilibrium position of the pest population is so low that the proportion of the crop destroyed either has no economic value, or it has a value that is less than the cost of chemical control.

This report, however, is not primarily concerned with the manipulation of equilibrium positions of pest populations to conserve crops. Instead, the author seeks to analyze those environmental agents that influence population densities and their attendant fluctuations—based on the proposition that all self-perpetuating persistent animal populations are subject to the same *basic* regulatory mechanisms. These studies are derived from continuing investigations of *Anagasta* ecosystems initiated by Flanders and Badgley (1963).

These ecosystems demonstrated the natural tendency of self-perpetuating populations to maintain relatively stable conditions (homeostasis). An ecosystem population is maintained by a sustained state of corrective reactions to disturbing forces (Nicholson, 1954). The disturbing forces in *Anagasta* ecosystems include food depletion, parasites, predators, pathogens, and occasional invasions of insect species that compete for the food supply. As Chapman (1927) pointed out, laboratory studies of such relations could lead to a better understanding of homeostatic conditions in nature. One means of realizing this objective is a study of ecosystems in which a natural enemy determines the density of its own population by determining the population density of its host.

THE EQUILIBRIUM POSITION

H. S. Smith (1929), while in charge of the biological control of agricultural pests for the state of California, pointed out that in practical work we are only casually interested in a natural enemy's ability to increase in numbers; our vital interest is in its equilibrium position—that is, the numerical "level" of its population and that of its prey. As is well known, the average rate of population increase in a homeostatic situation is

zero, the death rate being equal to the birth rate (Smith, 1937).

Herbert Spencer in his *First Principles* regarded the acting and reacting processes of fully developed societies as involved combinations of rhythms, characterized by an average condition which remained practically constant during the deviations ever taking place on opposite sides of it.

Under natural conditions, as pointed

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out by Nicholson (1947), a population's rhythm may be extrinsic in origin; that is, it is established by annual fluctuations in climate. However, climate-induced fluctuations, when superimposed on the complex system of population balance, tend to mask the intrinsic origins of fluctuations. Supporting the whole system, of course, are the environmental and evolutionary factors that, together, have determined which plants and animals can live and react together and have given those populations their specific properties. Nevertheless, the numerical level of population balance depends largely on either the population's use of food or on its serving as food (Flanders and Badgley, 1963).

Smith (1937) considered the equilibrium position of a population to be the most important of all biological phenomena. In the *Anagasta* ecosystems, the equilibrium position is a function of the food-finding capacities of the populations, as determined by the physiological attributes of the individual and the intra- and interspecific competition for food and space. When natural enemies are present, it may be a function of the rate at which natural enemy-caused host mortality increases and decreases with host density. This rate, in turn, is the function of the prey-finding (thus reproductive) capacity of the natural-enemy population.

The search for formulae to predict a population's ultimate homeostasis is likely to be futile if such formulae are based on the physiological attributes of the individual, since environmental circumstances preclude the full expression of such attributes.

Criteria for the homeostasis of host-parasite interactions can not be ascertained by means of life-table studies—vital statistics merely being the result of population reproductivity, not the

means by which population levels are attained. The only pertinent data relating to the attainment of host-parasite homeostasis is derived from mechanisms of host protection that influence the extent of the parasites' host-regulative capacity. This conclusion is based on two axioms: (1) that parasite species characterized by high inherent fecundity² are so characterized in order to counteract their relatively low host-finding capacity; and (2) that species in balance with their host populations rarely, if ever, realize their reproductive capacities.

If a population's equilibrium position extends over a period of seven generations or more, as in the *Anagasta* ecosystems, the average number of individuals attaining reproductive maturity equals the number of their parents. The surplus individuals are destroyed either by starvation, disease, or natural enemies. Woodworth (1908) suggested that each regulating action produces its own particular point of balance; at maximum effectiveness of a natural enemy, only those hosts survive that are needed to maintain the species. He also noted that the efficacy of a natural enemy against one host species may be profoundly influenced by the "ups and downs" of other host species.

Smith (1935) stated that population fluctuations generally are solely dependent upon the chronological distribution of variations in the ratio of births to deaths and occur regardless of the equilibrium position; such variations are inherent to the biology of the species.

Nicholson (1947) pointed out that (1) unlike unicellular animals, offspring of multicellular animals begin to add their demands for food to those of the parent stock only after a lapse of some time; and (2) this delayed response of animal density to the condi-

² The inherent fecundity of a species is the lifetime reproductive capacity of the average female that would prevail in the absence of environmental resistance.

tions of the food supply inevitably gives rise to very obvious fluctuations when stabilizing factors are absent. Nicholson also suggests that reproduction in multicellular animals continues even when food becomes scarce. Such reproduction is stabilized by difficulty in finding food or the consequent migration of the surplus into habitats vulnerable to natural enemies.

The lack of emigration and immigration of individuals from the laboratory ecosystems represents the "equilibrium" of such migrations in nature (Sellers, 1953).

An *Anagasta* ecosystem population in a constant environment attains an equilibrium position with characteristic fluctuations (figs. 1 through 10)³ when initiated with a continuous sequence of single reproductive individuals of natural enemy and prey and a series of food allotments sufficiently small in number to enable the developing populations to quickly accommodate themselves to their habitat. As a consequence, the natural enemy-prey rela-

tion in each ecosystem is a continuous process.

An *Anagasta* population's capacity for "habitat accommodation" necessarily includes social behavior that tends to prevent over-exploitation of the food supply but not eventually its complete utilization. Lack of complete utilization is a function of prey-regulative natural enemies.

Prey-regulative natural enemies, when reducing their prey populations, so reduce their own that they allow accessible prey to escape. Regulation efficiency is measured by the amount of food conserved (tables 1 through 6). This varies from none to 25 per cent or more of the original amount when the rotation period (episode age) is one year or less.

Behavioral differences in initial host populations that inhabit the original food allotments may preclude an exact replication of an ecosystem. The equilibrium positions attained, however, are comparable (fig. 10).

PERTINENT BIOLOGICAL CHARACTERISTICS

The ecosystems consist of populations of the grain-infesting moth *Anagasta kuehniella* (Zeller) associated with one or more populations of the following natural enemies: the predatory (egg-feeding) mite *Blattisocius tarsalis* (Berlese), the endoparasitic (larva-feeding) wasp *Devorgilla canescens* (Gravenhorst), and the bacterium (larva-infecting) *Bacillus* sp. nr. *thuringiensis* Berliner. They are maintained in an almost constant environment (temperature, approximately 80°F; relative humidity, approximately 55 per cent) and regularly provided with constant amounts of food (nonviable rolled wheat in the form of flakes).

Each food allotment of 120 grains of

wheat (7.7 grams) in its receptacle serves as a habitat for the developmental stages of all organisms. The initial habitat depth ranges from 3 mm to 42 mm in the different ecosystems. Habitat depth influences the host-searching efficiency of the natural enemies of *Anagasta* and consequently is a critical factor in determining the equilibrium positions of their populations. Since each habitat is temporary, it forms an episode in the life of the ecosystem. Each habitat allotment remains in the ecosystem for 24 weeks, unless the natural enemies are so efficient that the food conserved will support the host for an additional 24 weeks, as in Ecosystems XVII⁴ (table 3), XIVA (table 5), XV

³ See center-fold pages for all figures and tables.

⁴ Roman numerals alone are used hereafter to identify ecosystems used in this study.

(table 6), and II plus V (fig. 7). (II and V were joined so that the adult organisms could move freely from one to the other.)

The number of consecutive generations per episode varies inversely with the rate at which the food is utilized. Host generations vary from one to eight; parasites, one to 18; and predators, one to 36. The sequential food replacements ensure enough overlapping of prey to maintain natural enemy populations, despite the tendency of natural enemies to counteract such overlapping (Flanders, 1965).

An analysis of removed habitat allotments from ecosystems inhabited by *Devorgilla* showed roughly the following relationships between each allotment weight (in grains) the number of *Anagasta* cocoons:

Grains:	30	40	50	60	70	80	90	100
Cocoons:	95	80	75	55	45	35	25	15

Since each habitat allotment is originally free of life, the growth of the host population precedes that of the natural enemies. If both parasite and predator are present in the ecosystem, the growth of the predator population precedes that of the parasite—the former attacking only the host egg, the latter only the larvae and prepupae. Consequently, the episodal growth curves of the several populations within an allotment do not coincide, but lag one after the other. In a given host population that is even-brooded (all individuals are the same age) the emergence of adult hosts and parasites tends to coincide, provided that the parental parasites had oviposited in half-grown host individuals (Flanders and Badgley, 1963). When wheat depletion determines the equilibrium position, the emergence of *Anagasta* adults from a single habitat allotment begins during the seventh week and extends for about

seven more weeks; emergence is complete after all the food is utilized.

In ecosystems in which the equilibrium position of the host population is determined by wheat depletion, the fixed amount of food that circumscribes each episode is usually completely utilized in nine weeks. The allotment residue, however, is not removed until 15 weeks later. The characteristic equilibrium positions are maintained by the continuous food supply of each population-saturated ecosystem (figs. 2,3,4,7,8).

In ecosystems in which the equilibrium position is parasite-determined, the food in each allotment is very slowly utilized. Consequently, the allotment is replaced by fresh wheat after it has formed part of the ecosystem for 48 weeks (figs. 3,5,6,7,10).

Allowing allotments to remain in such an ecosystem for periods up to 100 weeks permits the parasite to destroy the ecosystem completely, although each allotment still contains a considerable amount of food. The prolonged sub-surface larval feeding and the consequent accumulation of spoor decrease the depth of this food to a point below the "threshold of protection." Then, all host larvae are constantly within the parasite's reach. This was demonstrated in I M₂ (fig. 2), which was initiated January 15, 1960, and five years later in August, 1965, was annihilated by parasites.

The graphs of the populations depicted in XIII (fig. 7) show the appearance and the gradual disappearance of lag in the parasite population growth curves relative to those of the host. These phenomena followed the introduction of the parasite into a host population that was being regulated by predators (fig. 11, Flanders and Badgley, 1963.) The consequent surge of parasitism that began about January 15, 1961, and extended for about 80 days resulted in the annihilation of the

host population. Ecosystem XIIIIM (fig. 7) was then initiated with the introduction of 12 *Anagasta* females. Ordinarily, the depths of the habitat allotments, such as those in XIII and XIIIIM, provide the *Anagasta* larvae with enough protection from parasitic attack so that the prey can be continuously regulated either by joint predator-parasite action or by predation alone.

The lack of lag in a parasite-regulated ecosystem is depicted in II plus V (fig. 7). The occurrence of a definite lag in the growth cycles of host and parasite is correlated with host increases that are independent of natural enemy action. Thus, in IX (fig. 8) the peak of the parasite cycle follows that of the host by 10 to 15 days.

It is evident, therefore, that the lag of parasite population growth curves tends to disappear as host regulation by the parasite increases in efficiency.

Ecosystems in which the equilibrium positions are predator-determined are exemplified by XVII (table 3) and its duplicate, VIIIB (table 1 and fig. 1, Flanders and Hall, 1965). The low equilibrium position depicted in the graph of XVII (fig. 3) during the first 400 days is similar to that which occurred during an equal period in VIIIB during 1965-1966. In none of the ecosystems has the predator annihilated its prey, this apparently being precluded by the relatively high prey density needed to sustain a predator population.

The permanence of *Anagasta* ecosystems in which natural enemies are present but not prey-regulative depends on the rate of food replenishment and internequine larval strife. It is apparent that the equilibrium positions of interacting natural enemies and the prey respond to these events. Population explosions and self-extermination do not occur in well balanced ecosystems as long as additional species are not introduced. The limitation of *Anagasta* pop-

ulations by food depletion and territoriality is precluded by the prey-regulative action of natural enemies. Natural enemies, by such action, secondarily reduce their own populations to a point where the proportion of accessible prey that escape attack is increased.

Such prey-predator regulation is possible only when the search for prey is largely limited by tropic responses to a zone (the surface layer of the habitat (allotments) in which the prey eggs are concentrated. Parasite regulation (when special protection devices are absent) operates only when each allotment consists of wheat flakes between 7 and 9 mm deep (the threshold of protection in ecosystems with 24 habitat allotments).

If a natural enemy should increase excessively in ecosystems such as III (fig. 3) and IX (fig. 2), where the individual prey for most of its susceptible stages is afforded absolute, rather than fortuitous, protection, the equilibrium positions of the prey would show little, if any, change, since there is a great surplus of prey. However, if a natural enemy should increase excessively in ecosystems such as XVII (fig. 3) and XV (fig. 6), where normally it is prey-regulative (prey protection not being absolute but determined by chance), the effect would be detrimental from the standpoint of ecosystem perpetuation. With XV the effect could be annihilative, both to the prey and parasite. As noted below, doubling the area that can be effectively searched may not consistently double the number of hosts found by the parasite. A decrease in the percentage of successful searching may result ultimately in an excessive increase of the parasite population.

This conclusion is based on observations of XIII (fig. 7) in which the original population was annihilated during March, 1961, by an excessively abundant parasite population. Over-exploitation of the prey began about

December 20, 1960, and prevailed for 60 days. The parasite population which originated from one individual introduced early in September, 1960, became excessive within five generations. If host and parasite develop simultaneously from very small numbers, a wheat allotment depth of 10 mm, as in this ecosystem, ordinarily gives the larval prey population sufficient protection from annihilation by parasites.

In XX (fig. 8), which was initiated April, 1965 with 48 habitat allotments,

the depth of each (7.5 mm) proved to be insufficient to provide any *Anagasta* larvae life-time fortuitous protection from parasitic attack, the *Anagasta* population being annihilated in eight host generations. However, lifetime fortuitous protection of a new *Anagasta* population, initiated with six females, was obtained by placing on the surface of each allotment a 12-mm glass disc. The initial evidence for ecosystem annihilation is the absence of coexisting live *Anagasta* adults of both sexes during a 70-day period.

INVASION BY *TRIBOLIUM CONFUSUM*

Ecosystems in which the parasitic regulation of the *Anagasta* population is so effective that the predator population is largely eliminated by starvation are subject to successful invasion by the beetle *Tribolium confusum* Jacquelin duVal. Under certain conditions, reproduction by the beetle, when added to that of the parasite, can annihilate an ecosystem. The beetle probably accomplishes this either directly as a predator of the cocooned parasite or indirectly by sustaining a population of *Blattisocius* which reduces the egg population of *Anagasta* below the latter's survival level. Despite the opportunity to do so, *T. confusum* has not successfully invaded predator-inhabited ecosystems. When beetle adults were intentionally introduced into such ecosystems, reproduction did not occur.

Ecosystem XVIII was annihilated during September, 1966, by the combined action of *Tribolium* and *Devorgilla*. This ecosystem had been established in August, 1965, with 24 habitat allotments—two weeks to 48 weeks old—that had been removed from the II plus V. Allotments were 6.5 mm deep and 68 mm in diameter and occupied opaque containers. (The influence of opaque and translucent containers on predator action will be discussed later.)

Annihilation occurred despite protective cardboard discs 12 mm in diameter provided for each allotment when the ecosystem was established.

The end of this ecosystem was pre-saged by a marked increase in the final weights of the replaced one-year-old allotments. The average weight of the last eleven allotments to be removed was 93 grains, whereas the average weight of the preceding eight allotments was 75 grains, a weight more or less characteristic of the allotments in any *Anagasta* ecosystem whose populations are most efficiently parasite-regulated.

Tribolium first appeared in XVIII during September, 1965. From then on every *Tribolium* adult was destroyed at the time it was first observed. By the end of the year the average number destroyed per day was three; the total for September, 1966, was 60.

The daily routine of collecting the dead adult *Anagasta* showed that no *Anagasta* eggs were laid after July, the last of the mated *Anagasta* females having died July 24; the egg-predator *Blattisocius*, therefore, subsisted on the eggs of *Tribolium*. It appears, then, that in XVIII the predator population, supported largely by the beetle population, could have been partially, if not entirely, responsible for the elimination of

the *Anagasta* populations. The prerequisite of this effect was the parasitic regulation of *Anagasta* at low densities.

When this ecosystem became defunct, each of the 24 allotments was dissected and analyzed to ascertain the interrelations of *Tribolium* and *Anagasta* (table 8). The ages of these allotments varied from one to 47 weeks. Immediately after the *Anagasta* were annihilated, the numbers of *Tribolium* and of *Blattisocius* in each allotment habitat were counted (table 8). The analysis showed that only allotments that had been infested by *Anagasta* were inhabited by the beetle, and that their numbers per allotment tended to vary with the amount of *Anagasta* spoor. *Tribolium*, under these circumstances, were evidently attracted to *Anagasta*-infested wheat only.

Ecosystem XIVA in which the parasite had maintained the *Anagasta* population at very low densities for many generations, and had been inhabited by *Tribolium* only since April, 1965, became defunct in December, 1966.

The daily destruction of adult beetles when found outside the allotment habitats prolonged the life of XIVA over that of XVIII—possibly because allotment containers in XIVA were translucent, and those in XVIII were opaque.

Stanley and Grundman (1965) noted that the *Tribolium* females prefer a dark environment when ovipositing. It seems likely, therefore, that beetles inhabiting translucent containers are more prone to roam. This would permit the daily destruction of adults, so that reproduction is largely precluded.

As noted earlier, *Tribolium* can successfully invade an *Anagasta* ecosystem only when the parasite *Devorgilla* is so effective that the egg-predator *Blattisocius* is either absent or very scarce.

When such an invasion occurs and the predator action of *Tribolium* is added to parasitization by *Devorgilla*,

the entire *Anagasta* population—and that of its parasite are ultimately destroyed. This joint action of predator and parasite is detrimental to all the organisms concerned except *Tribolium* which can subsist very well on rolled wheat alone.

In XIVA the low density of the *Anagasta* population (fig. 5, table 5) and consequent lack of *Blattisocius* resulting from parasite regulation permitted the successful invasion of the ecosystem by *Tribolium* early in 1965, the first adult being observed March 10. The careful daily removal thereafter of all adults found outside the allotment habitats kept the *Tribolium* population from having any significant effect on the ecosystem for one and one-half years, the average number of beetle adults removed per month being seven. Suddenly this average increased to 64 for a three-month period (October, November, December, 1966), apparently an effect of inefficient collection that allowed adult beetles to remain in the ecosystems too long. This increase coincided with the complete destruction of the *Anagasta* population and of its parasite. The last of the mated females died October 19; the last parasite died December 19.

The ecosystem, which then consisted only of the *Tribolium* population subsiding on wheat flakes, was restocked with *Anagasta* by introducing two mated females on December 25, 1966. The adult progeny of the new line of *Anagasta* began to emerge February 11, 1967, despite the presence of *Tribolium*. This generation, consisting of 125 adults, proceeded to emerge for the next 37 days, their life-cycles ranging from 47 to 84 days.

Since *Blattisocius* had not survived in the ecosystem on the eggs of *Tribolium* alone, as evidenced by the lack of phoretic individuals on the early emerging adult *Anagasta*, it was introduced concurrently with the emergence of the

latter. The number of *Tribolium* collected monthly decreased from 26 in January to five in July. This was probably an effect of egg-eating by *Blattisocius*; the moth-mite ratio was 1:3. (During 1967, a total of 126 adult *Tribolium* were captured in restocked XIVA, a period in which 1,520 adult *Anagasta* emerged. Because of *Blattisocius* predation, *Tribolium* completely disappeared from this ecosystem during 1968.)

Two identical ecosystems were initiated November 4, 1965, to ascertain the effects of possible biological differences in the inocula (XXII and XXIII; fig. 10, table 9). The gradual accretion of the food supply and the population dependent thereon began with two standard wheat allotments, 9 mm deep and 56 mm in diameter in each ecosystem. These dimensions were determined by the size of the translucent plastic (polystyrene) container. Two allotments were added to each ecosystem weekly for 23 weeks.

Two mated female *Anagasta* and two female *Devorgilla* were maintained in each ecosystem, being replaced upon death, until the adult progenies of the initial female began to emerge 42 days later.

When the number of allotment habitats in each ecosystem reached 48, two 48-week-old allotments were removed each fortnight. As in all ecosystems, each allotment was carefully weighed in order to ascertain the amount of wheat conserved by the action of the natural enemies of *Anagasta*.

The population graphs for the two ecosystems over a period of 505 days beginning 20 weeks after ecosystem initiation (fig. 10) show distinct biological differences, which apparently originated from reproductive differences in the inocula, particularly of *Anagasta* (table 9).

The graphs show that the reproductivity of the inoculum was greater in XXII than in XXIII. The population repercussions of this difference are given in table 9.

The relatively high parasitization in XXII facilitated the invasion of the ecosystem by *Tribolium*. The predatory activity of the beetle following its establishment reduced the parasitization, but at the same time it destroyed enough additional *Anagasta* to increase the conservation of the wheat supply during the year by 11 grains per allotment. As in all ecosystems where populations were regulated by the parasite, the ratio of *Blattisocius* to *Anagasta* was extremely low, less than one *Blattisocius* to ten or more *Anagasta*. However, in XXII, for a brief period when about 100 adults of *Tribolium* were present, the average number of *Blattisocius* carried by an *Anagasta* adult was 2.3, this number having developed upon the eggs supplied by *Tribolium*.

The bacterium *Bacillus thuringiensis* was present in XXII and XXIII, despite the general absence of competition among the *Anagasta* larvae in the 48 allotment habitats of each ecosystem. The number of diseased larvae in removed 48-week-old allotments ranged from one or two to about 30. The oviposition action of the parasite in transmitting the bacterium appears responsible for the noticeable presence of the disease (Flanders and Hall, 1965). The influence of the bacterium in population control was negligible.

Conditions of larval stress conducive to epizootics of *Bacillus* occurred only briefly, as in XXIII, when an average of 300 larvae became full-fed on each of several days (fig. 10). The stress was evident during this period when 235 larvae—most of them diseased—emigrated from the allotment habitats.

NATURAL ENEMY INTERACTIONS

The equilibrium positions and population fluctuations in these *Anagasta* ecosystems, depicted in the graphs of figures 1 through 10, are designated: "wheat-depletion," "parasite," "predator," "predator and parasite," or "bacillus-parasite"—depending on the factor that most significantly influenced the conservation of wheat. For example, the equilibrium positions in I and IV (fig. 1) are "predator and parasite-determined," although each includes periods when wheat depletion was a factor.

The physical and biological factors characterizing the various populations for the selected life-periods are presented in tables 1 through 6.

The critical physical factor is the configuration of the habitat allotments; the critical biological factor is the intraspecific competition for food by *Anagasta*, by its parasite, or by its predator. Together, these factors determine the availability and variability of the food supply. The depth of the habitat allotments determines, in effect, the *searching* efficiency of the natural enemies. The inherent searching capacity of a natural enemy, of course, does not change, but it is a specific constant that may be realized only under conditions favorable for host-finding and in the absence of competition, either intra- or interspecific. The actual *prey-finding* efficiency of a natural enemy is indicated by the annual ratio of adult prey to adult natural enemy. The ratios characterizing the ecosystems and given in tables 1 through 6 range as follows:

Female host-parasite ratios: 4.0:3.0 in IX (table 2) and 1.0:24.0 in I M₂ (table 6). The host-parasite ratios represented by the graphs of XX (fig. 8) are 1.0:31.0 for the parasite-annihilated population and 1.0:17.0 for the parasite-regulated population.

However, the prey-predator ratios

that are significant with respect to the predator's prey-regulative efficiency are the *minimum* ratios computed for periods of at least three weeks by counting phoretic predators on about five adult moths each week. This three-week period of counting is necessary, because (1) the predator population, unlike the populations of the prey and the parasite, cannot be ascertained each day by counting dead adults; and (2) the number of adult predators carried by an individual adult moth varies inversely with the relatively rapid changes in the densities of the moth population (Flanders and Badgley, 1963).

The minimum prey-predator ratio in IX (table 2) in which the equilibrium position is wheat-determined is 1.0:0.6; that in XVII (table 3) in which the equilibrium position is predator-determined is 1.0:1.0. The range in number of predators per weekly moth sample for a 70-week period was 0.2 to 12 in IX and 0.5 to 27 in XVII. In XII (table 4), in which the predator is prey-regulative for only about one-third of the time, the minimum ratio for the three-week period was 1.0:0.23. In this ecosystem the number of predators per weekly moth sample for 70 weeks ranged from none to 47.

Analyses of prey-predator ratios in XVII (table 3) and VIIIB (table 7), in which the predator has been continually regulative for over two years, and in which such regulation as measured by the amount of wheat conserved varied from a low to a high period every 12 months, show that low efficiency is characterized by a 100-day period with average ratios less than 1:2.5.

Flanders and Badgley (1963) concluded that the predator is continually regulative only when the habitat allotment depths are between 2 and 8 mm.

It appeared that when several allotments had accumulated unusual amounts of *Anagasta* spoor, because of a temporary decrease in the predator's efficiency, the restoration of the low equilibrium position may be delayed.

The variability in predator-prey regulative efficiency increases as the depth of the allotments increase above 8 mm. In XVI, where for different periods wheat depths were 20 mm and 42 mm, the predator was prey-regulative for about 50 per cent of the time, the equilibrium positions of the prey populations being determined alternately by wheat depletion and by predation, with three prey generations for each determination. Maximum predation efficiency occurred when the wheat depth was 3 mm as in VIIIB. Each allotment was 120 grains and was replaced every six months. (See fig. 3 by Flanders and Hall, 1965.) This efficient prey-regulation by the predator also occurred in XVII (fig. 3) when it duplicated VIIIB. In both ecosystems, however, 250- to 300-day periods of full control alternated with 150- to 200-day periods of only partial control.

When an *Anagasta* population is regulated by predator-parasite cooperation, the number of *Anagasta* that at-

tain the adult stage occasionally may be double that occurring when the food supply is the limiting factor (discussion of Ecosystem I, Flanders and Badgley, 1960). In this event, the predator is practically absent, and the parasite population is nonprey-regulative; that is, it is in nonreciprocal balance—an effect of prey protection being excessive.

This difference was manifested in two consecutive 13-month periods: March, 1957, through March, 1958, a period of predator-parasite cooperation or "mite-affected phase," during which 1,756 *Anagasta* larvae became adult; and April, 1958, through April, 1959, a "mite-unaffected phase," when aramite was applied. The aramite practically eliminated the predator and caused the food supply to become limiting. In this period, only 883 larvae became adult.

After aramite treatments stopped, the predator and the parasite population again became cooperatively prey-regulative, the adult *Anagasta* population regaining its double number (I M₂, fig. 9). This increase may be, in part, caused by decreased parasitization and, in part, by periodic depletion of wheat, of *Anagasta* eggs and, therefore, of *Blattisocius*.

GRAPH ANALYSES⁵

Graphs of I and IV (fig. 1) represent populations at equilibrium positions that conserved 10 to 15 per cent of the wheat supply. The high equilibrium positions at the beginning and at the end of graph I occurred during periods when predators and parasites were not prey-regulative. At the beginning, fresh wheat was added once to each habitat allotment to retard the decrease in allotment depth as wheat was

consumed by *Anagasta* larvae. This ended on March 1, 1957, and the last of such allotments was replaced August 10, 1957. Prey regulation at the end was prevented by aramite application beginning November 14, 1957 (Flanders and Badgley, 1960). These high equilibrium positions were similar to those in the graphs of X and XII (fig. 4) that depict population levels at which prey regulation by natural

⁵ Two unparasitized larvae can use as much food as three parasitized larvae. This was not considered in the preparation of the graphs and tables for this report. To evaluate the data correctly, the author suggests that the number of highly parasitized larvae be reduced by one-third.

enemies was generally either absent or low; food conservation was 6 per cent or less.

The nadirs of the short prey-regulative periods of X and XII, as indicated by the lower equilibrium positions, were not so low as those of the prolonged like periods in XVII (fig. 3). Here, the 3-mm depth of the habitat allotments permitted effective regulation by *Blattisocius* by confining prey-searching to the prey-inhabited zone, despite the translucent containers. Food conservation amounted to 30 per cent—the maximum amount for ecosystems in which the habitat allotments remained for only six months. Less food was conserved when food was thus exposed for periods of nine months or more. As stated by Flanders and Badgley (1963), the allotment habitats should be removed before the spoor of *Anagasta* accumulates to the point that it may prevent regulation by the predator.

With the opaque containers, light was admitted only through the top surfaces where *Anagasta* eggs were concentrated. Regulation was achieved apparently because predators wasted less time looking for prey. Food conserved in the opaque habitat containers of I and IV (fig. 1) was over twice that in the translucent containers of X and XII (fig. 4).

The prey-regulative role of the predators in IV was shown by the notable outbreak of 588 full-fed larvae (the progeny of 15 *Anagasta* females) during a five-day period. Predators had starved for a 16-day period beginning 50 days before the outbreak, because the nine potential *Anagasta* adults that would have provided eggs to sustain the predators were, as a result of parasitization during their larval stages, replaced by nine adult parasites.

When the predator population in I (fig. 9), that for a year had been kept at very low levels by application of ara-

mite, was allowed to increase by being transferred to an aramite-free environment, its egg-feeding action (plus parasitization) reduced the average number of larvae that became full-fed each day from 13.7 to 12.0. Parasitization correspondingly dropped from 86.7 to 78.7 per cent. This, as is shown by the data for I (fig. 9), decreased the number of larvae that became full-fed each day, but simultaneously accentuated the periodicity of fluctuation of their populations and increased the amplitudes of such fluctuations. This phenomenon was caused apparently by the short periods in which the predator was almost completely eliminated from the ecosystem when parasite adults were substituted for *Anagasta* adults.

The periodicity of the fluctuations in graph IV (fig. 1) is not as apparent as in I. Population control in IV probably was more efficient, since the area being searched for prey eggs was 32 mm in diameter instead of 44 mm. The periodicity in IV, when not regulated by natural enemies, was noticeable during the population explosion period. An average of seven larvae became full-fed daily—not including the explosion population.

Graphs of II and IX (fig. 2) represent populations regulated only by wheat depletion. Intraspecific competition of *Anagasta* larvae was such that no food was conserved. Populations of the predator and parasite were kept from regulatory activity by a zone of vermiculite that overlaid the wheat allotments. Consequently, each of these natural enemy populations was in non-reciprocal balance with the prey population. Neither was there a reciprocal balance of food and prey, since the food supply merely sets an upper limit to the number of adult prey. The food supply of the prey population was a constant "flow" and arbitrarily replenished at intervals equal to one-seventh of a prey generation.

NOTE

Two unparasitized larvae can use as much food as three parasitized larvae. This was not considered in the preparation of the graphs and tables for this report. To evaluate the data, reduce the number of highly parasitized larvae by one-third.

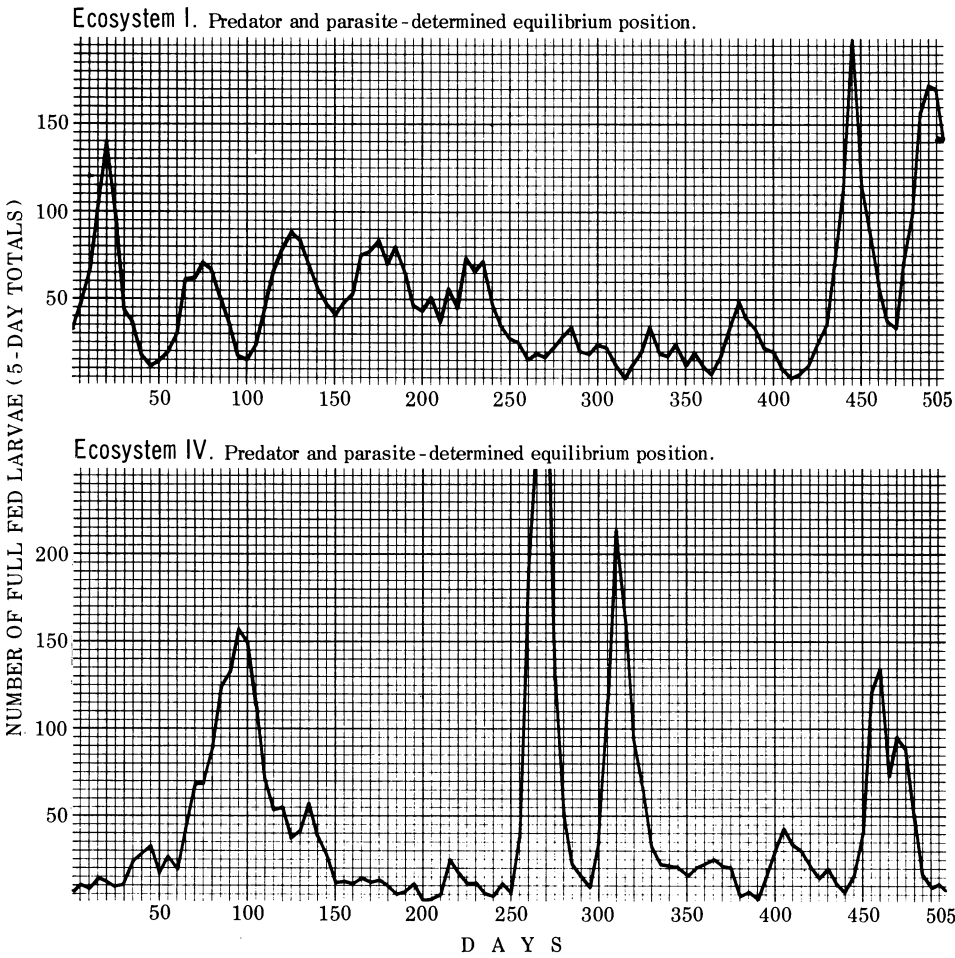


Fig. 1. Fluctuations of 10 generations of full-fed *Anagasta* larva populations and the equilibrium positions in 505-day segments of ecosystem life.

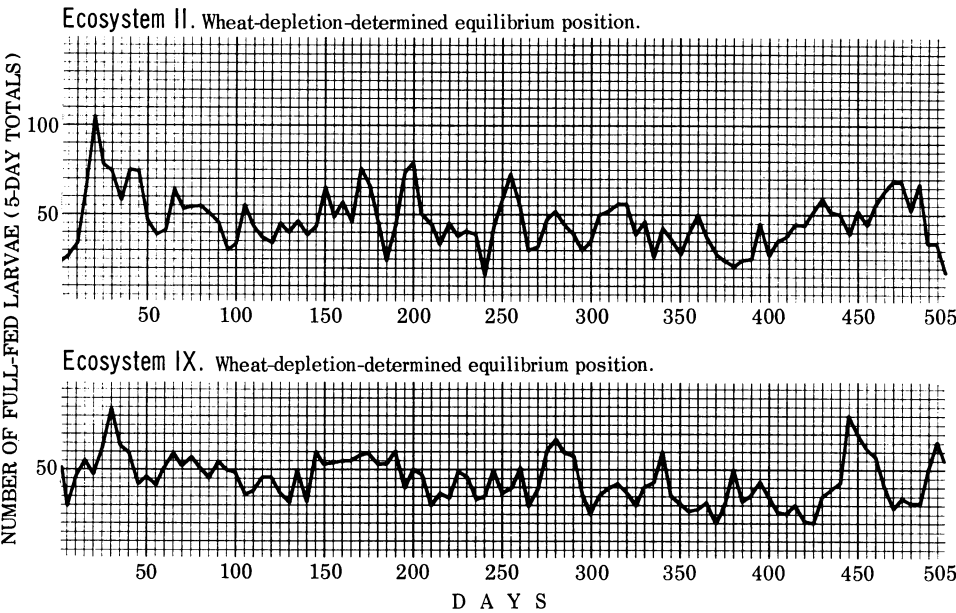


Fig. 2. Fluctuations of 10 generations of full-fed *Anagasta* larva populations and the equilibrium positions in 505-day segments of ecosystem life.

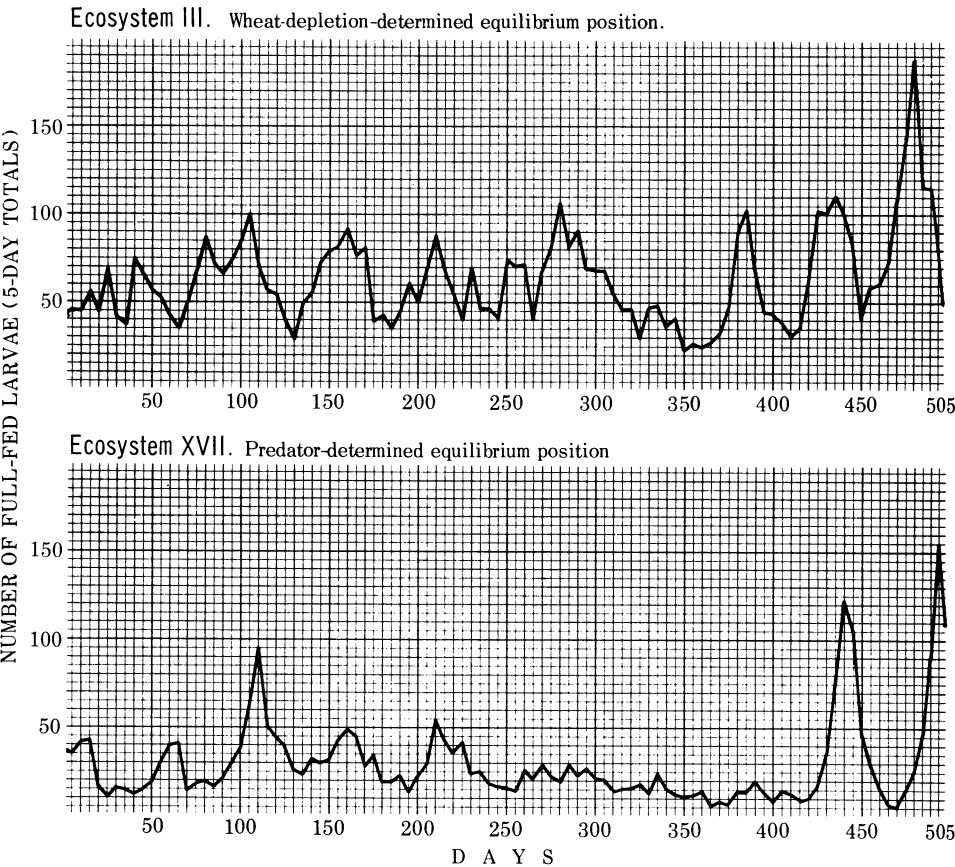


Fig. 3. Fluctuations of 10 generations of full-fed *Anagasta* larva populations and the equilibrium positions in 505-day segments of ecosystem life.

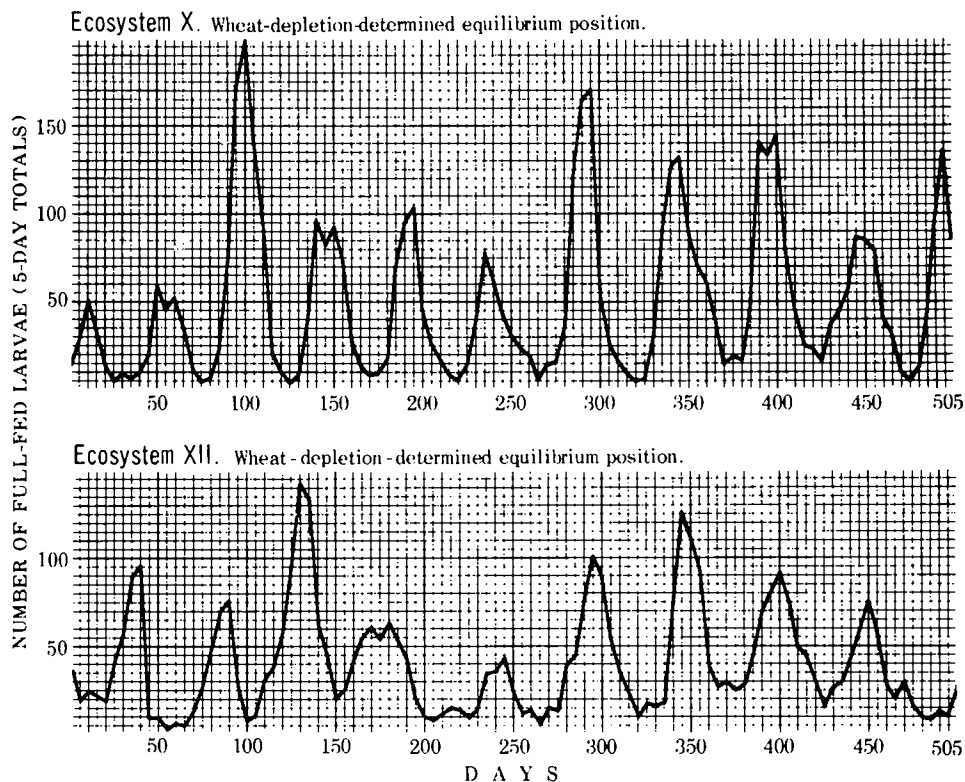


Fig. 4. Fluctuations of 10 generations of full-fed *Anagasta* larva populations and the equilibrium positions in 505-day segments of ecosystem life.

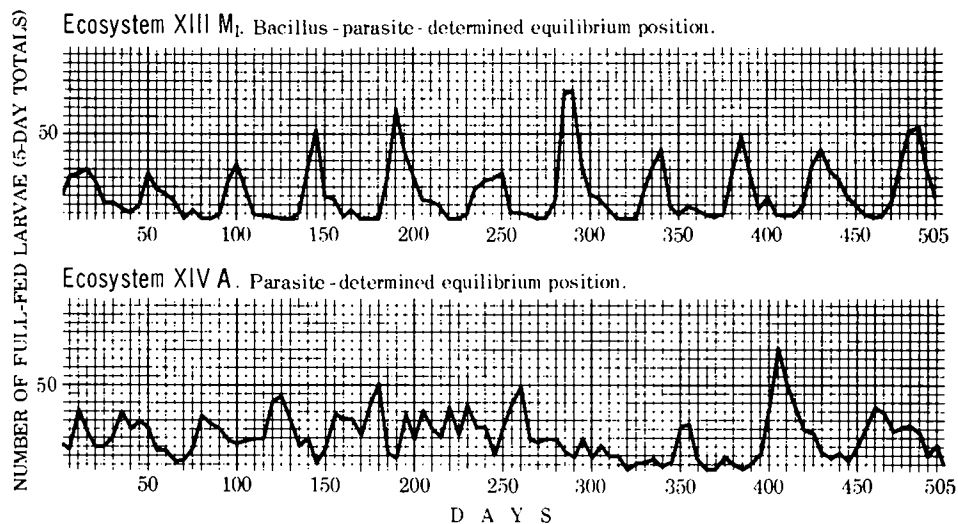


Fig. 5. Fluctuations of 10 generations of full-fed *Anagasta* larva populations and the equilibrium positions in 505-day segments of ecosystem life.

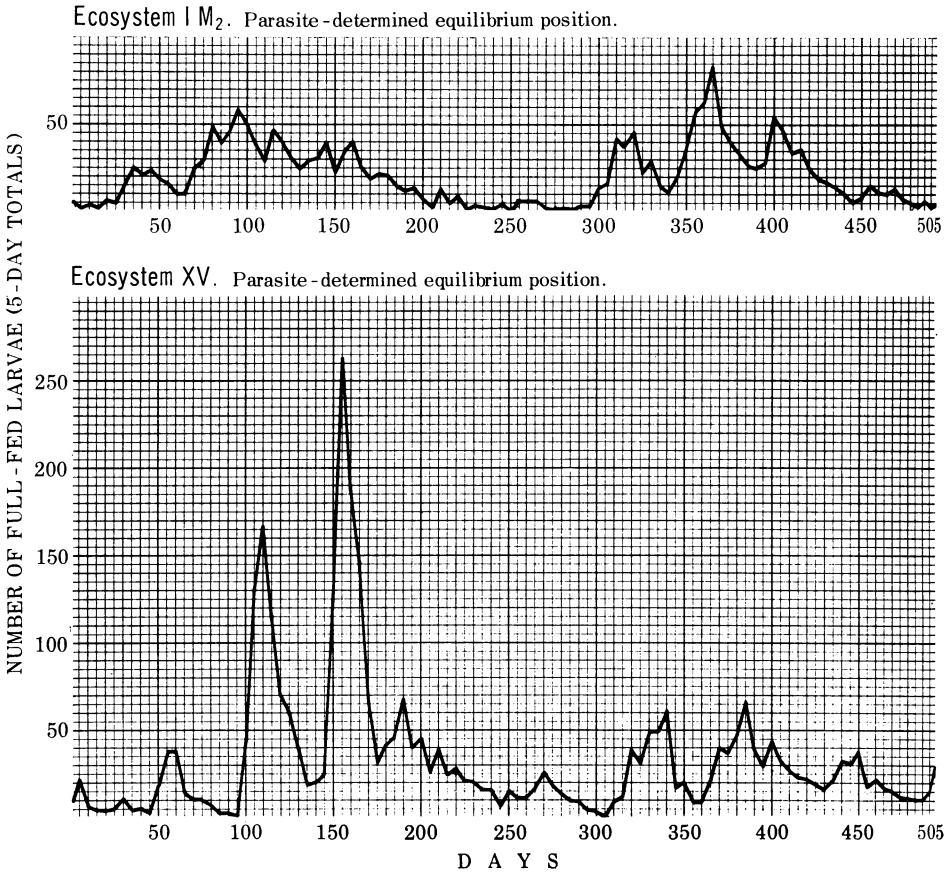


Fig. 6. Fluctuations of 10 generations of full-fed *Anagasta* larva populations and the equilibrium positions in 505-day segments of ecosystem life.

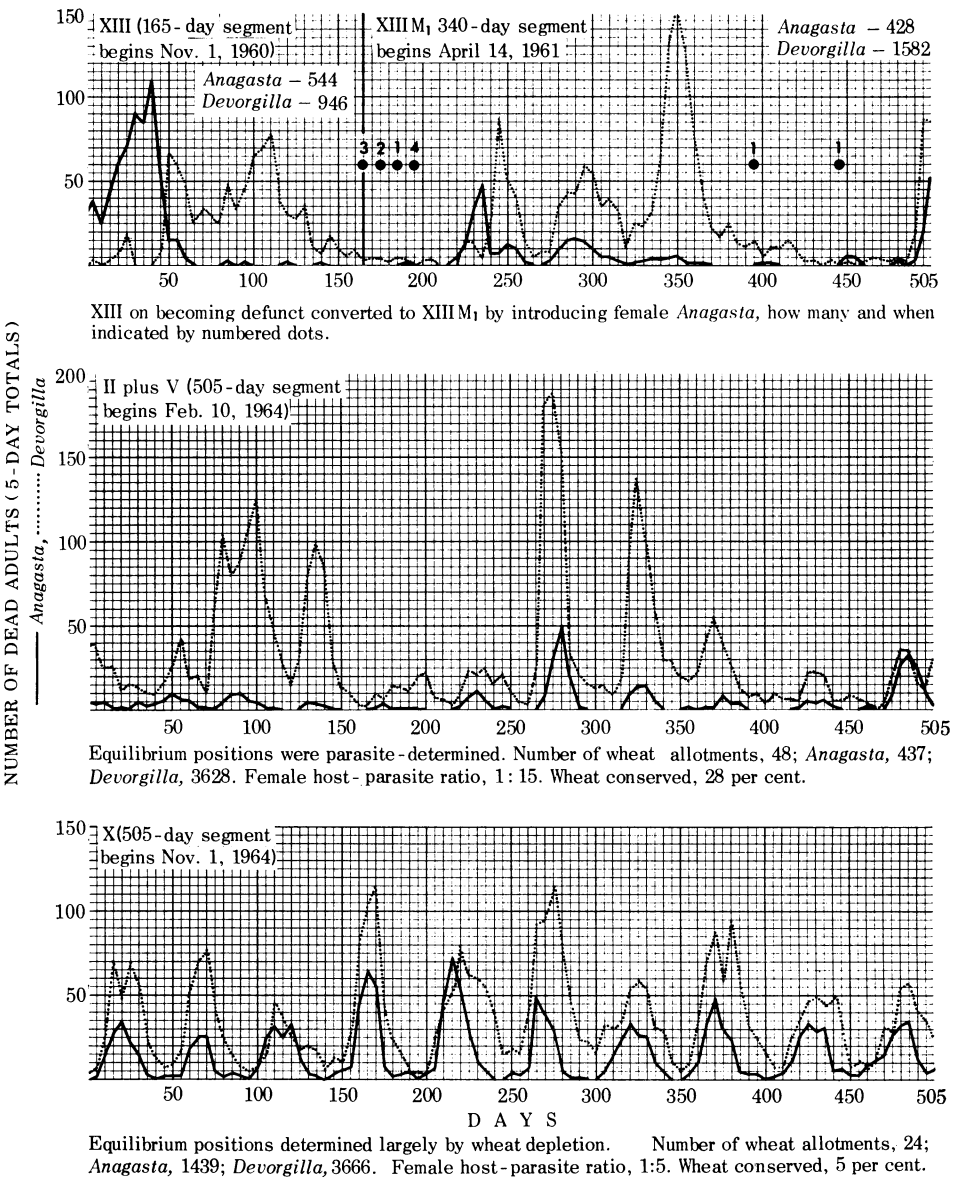


Fig. 7. Fluctuations of 10-generation populations of adult *Anagasta* and 20-generation populations of adult *Devorgilla*.

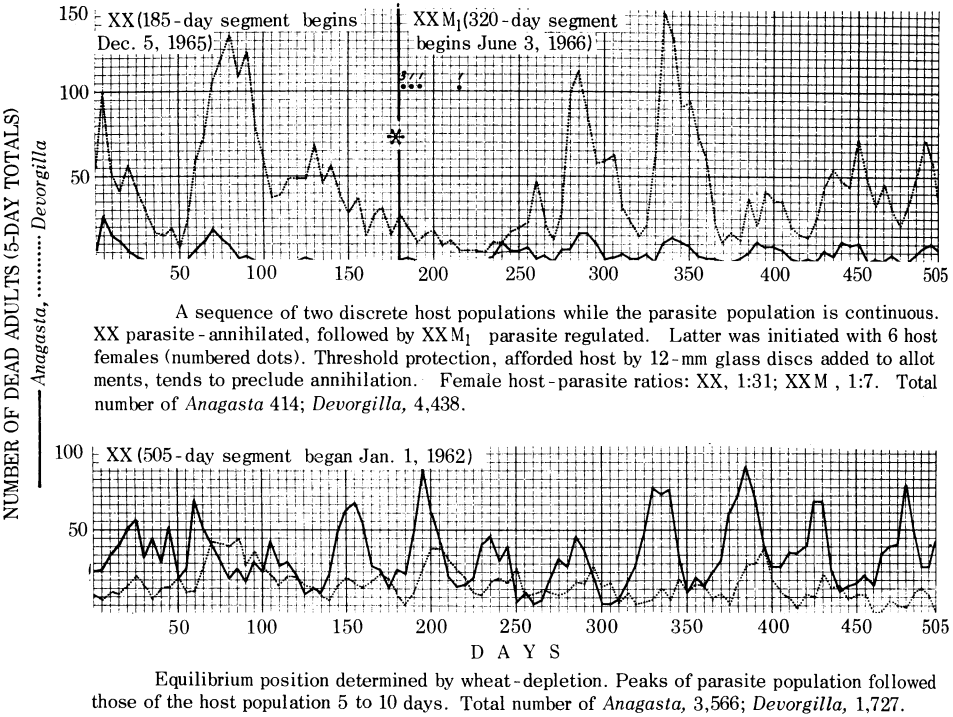
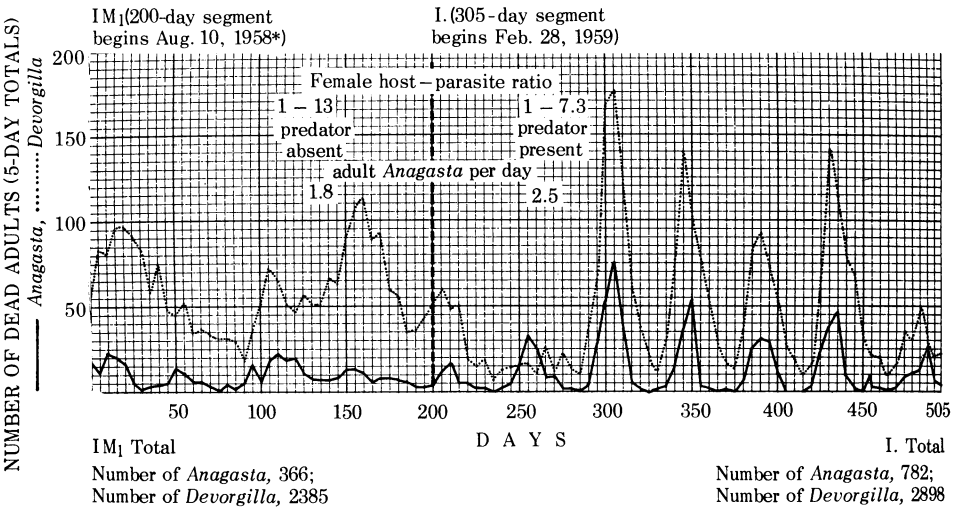


Fig. 8. Fluctuations of 10-generation populations of the adult *Anagasta* and 20-generation populations of the adult *Devorgilla*.



* Allotment containers treated with aramite. (Flanders and Badgley, 1960)

Fig. 9. Effect of predation on the periodicity and the amplitudes of an *Anagasta* population.

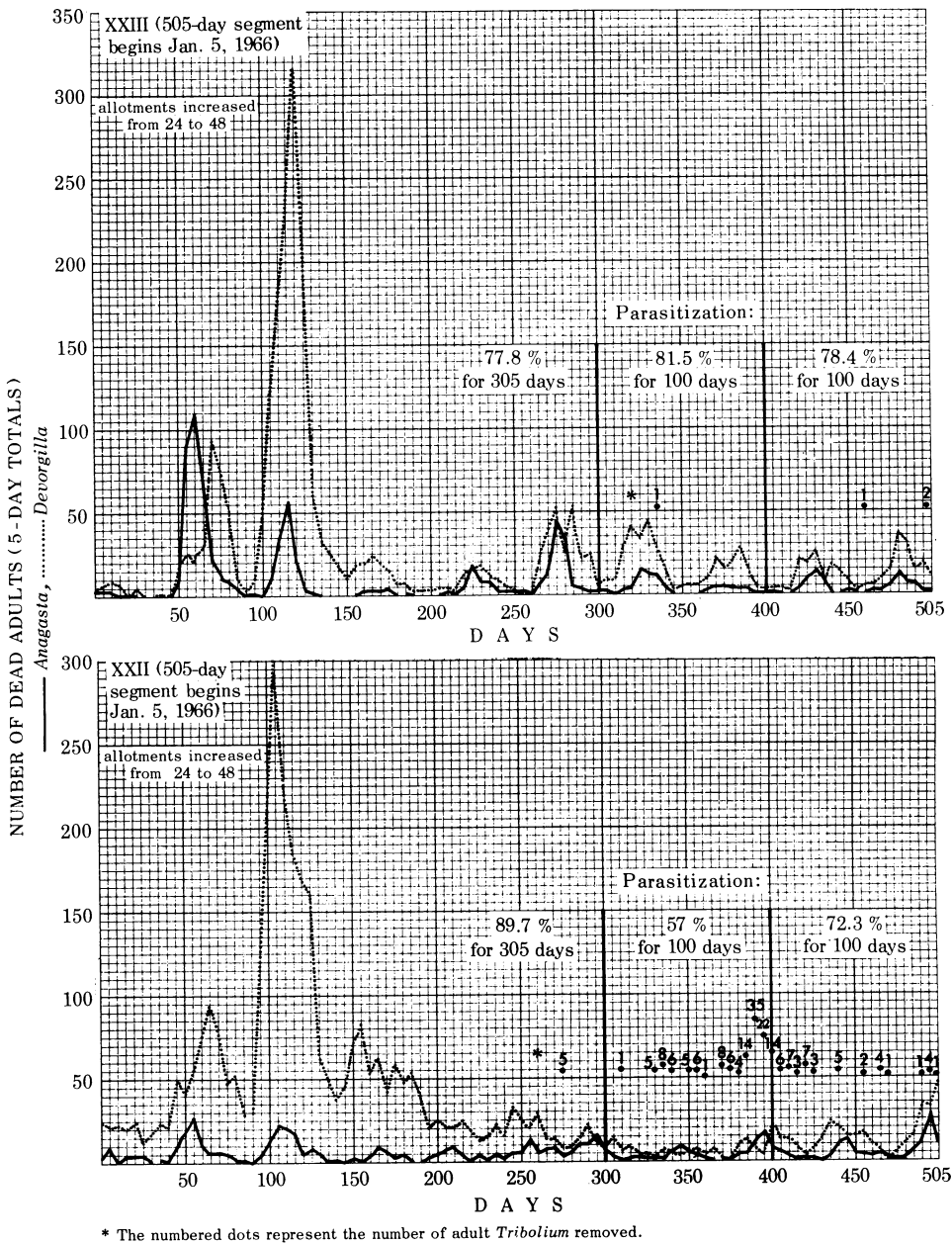


Fig. 10. Effect of predation by *Tribolium* larvae on per cent parasitization in two abiotically identical ecosystems. The numbered dots represent the number of adult *Tribolium* removed.

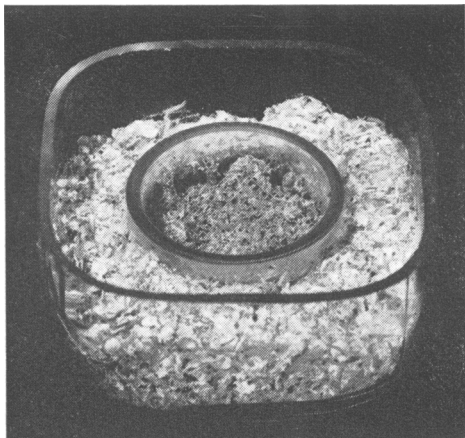


Fig. 11. About 1,000 freshly deposited eggs of *Anagasta* were isolated in a stender dish with 120 grains of wheat and surrounded by a wheat bank to receive excess larvae on February 21, 1966. Since internecine strife between the newly hatched and feeding larvae in this artificial infestation did not occur (as it would in natural infestations), the territorial effect was lacking, and the wheat was completely utilized in about four weeks instead of nine weeks—the minimum time required in wheat-regulated ecosystems. Photographed March 24, 1966.

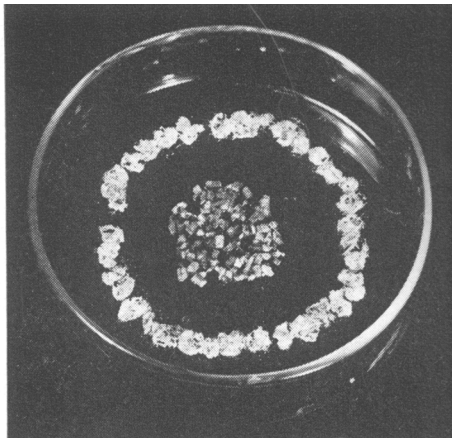


Fig. 12. About 1,000 *Anagasta* eggs were placed on a pile of vermiculite particles ringed with 35 wheat flakes in a petri dish on February 22, 1966. Vermiculite particles as well as the wheat flakes were firmly fastened to the dish by the silk strands of the newly hatched larvae during the process of establishing territories. A few of the larvae, when forced out from under the flakes by territorial action, found refuge in the mass of vermiculite; the others moved out of the petri dish. (Compare condition of wheat with that in stender dish in fig. 11). Photograph taken March 24, 1966.

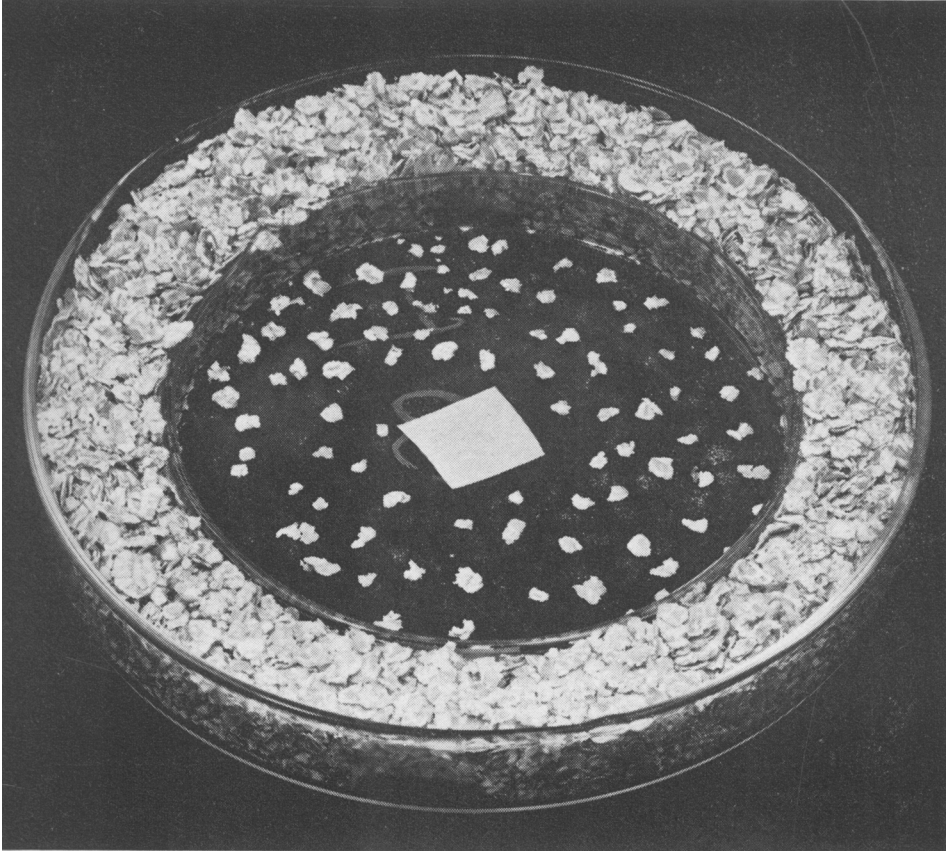


Fig. 13. A piece of paper holds about 1,000 *Anagasta* eggs—all the same age—surrounded by isolated flakes of wheat on floor of 10 cm petri dish. The bank of wheat flakes in outer petri dish harbors *Anagasta* larvae that are kept by territory action from taking shelter under the isolated wheat flakes. At a constant temperature of 80° F, the prolongation of the life cycles of the sheltered larvae beyond the average seemed to be at least equal to the periods of such shelter. The longest life cycle observed was 95 days; however, most ranged from 65 to 68 days.

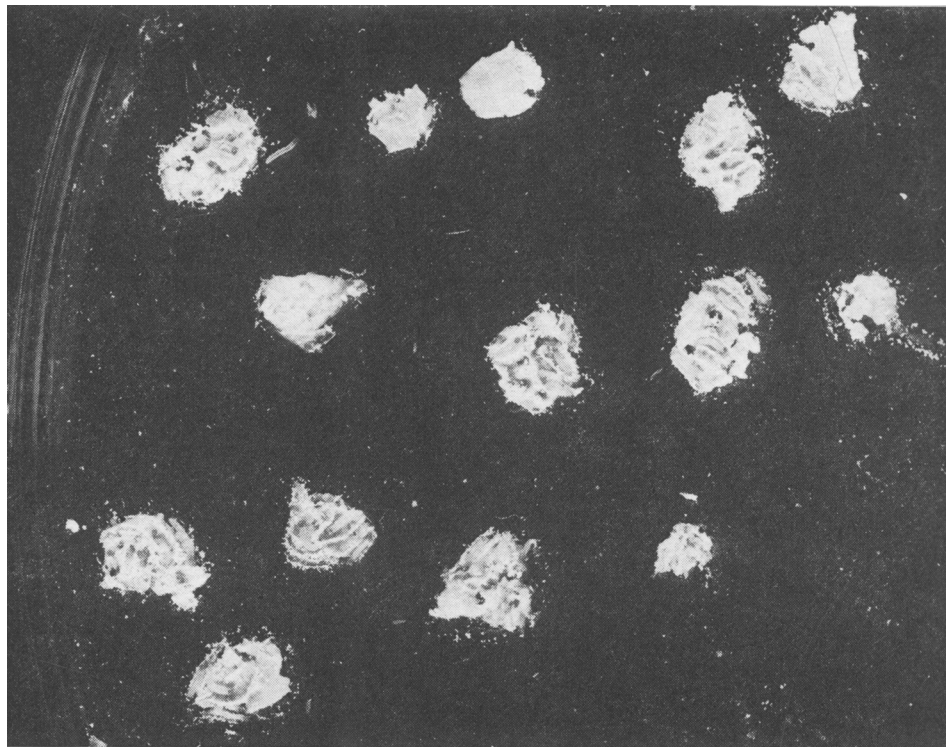


Fig. 14. Separate wheat flakes in petri dish occupied by newly hatched *Anagasta* larvae that have spun cocoons—isolating one from another.

TABLE 1
DATA ON ECOSYSTEMS DEPICTED BY CORRESPONDINGLY
NUMBERED GRAPHS

Item	Ecosystem I*	Ecosystem IV*
Segment of ecosystem life:		
Began.....	Dec. 21, 1956	Oct. 25, 1958
Years of life represented.....	1 and 2	2 and 3
Allotment characteristics:		
Composition.....	wheat only	wheat only
Dimensions (mm).....	14 deep, 44 dia.	28 deep, 32 dia.
Container.....	opaque	opaque
Full-fed <i>Anagasta</i> larvae:		
Total number (in 505 days).....	5,075 (nondiseased)	4,911 (nondiseased)
Daily average.....	10	10
Total per allotment.....	70	68
Natural enemies present:		
Type, number of generations.....	{ predator, 50 parasite, 20 predator and parasite, 190; intraspecific host competition, 315	{ predator, 50 parasite, 20 predator and parasite, 335; intraspecific host competition, 170
Regulative factors, periods of dominance (days).....		
Parasitized larvae (per cent).....	58	52.6
Adult female host: parasite (ratio).....	1:3	1:2
Average number of mature predators: adult host.....	(no record)	(no record)
Wheat conserved (per cent).....	14	15 (estimate)

* Twenty-four allotments, one replaced weekly.

TABLE 2
DATA ON ECOSYSTEMS DEPICTED BY CORRESPONDINGLY
NUMBERED GRAPHS

Item	Ecosystem II*	Ecosystem IX*
Segment of ecosystem life:		
Began.....	Mar. 10, 1960	Aug. 15, 1964
Years of life represented.....	3 and 4	8 and 9
Allotment characteristics:		
Composition.....	wheat with vermiculite overlay	wheat with vermiculite overlay
Dimensions (mm).....	{ wheat, 11 deep, 48 dia. vermiculite, 7 deep	{ wheat, 3 deep, 90 dia. vermiculite, 33 deep
Container.....	translucent	translucent
Full-fed <i>Anagasta</i> larvae:		
Total number (in 505 days).....	4,704 (disease incidence low)	4,497 (disease incidence low)
Daily average.....	9	9
Total per allotment.....	65	63
Natural enemies present:		
Type, number of generations.....	{ predator, 50; parasite, 20; bacterium, trace intraspecific host competition, 505	{ predator, 50 parasite, 20 intraspecific host competition, 505
Regulative factors, periods of dominance (days).....		
Parasitized larvae (per cent).....	55	30
Adult female host: parasite (ratio).....	1:2.5	4:3
Average number of mature predators: adult host.....	1	4
Wheat conserved (per cent).....	none	none

* Twenty-four allotments, one replaced weekly.

TABLE 3
DATA ON ECOSYSTEMS DEPICTED BY CORRESPONDINGLY
NUMBERED GRAPHS

Item	Ecosystem III*	Ecosystem XVII*
Segment of ecosystem life:		
Began.....	July 10, 1961	Sept. 30, 1964
Years of life represented.....	4 and 5	1 and 2
Allotment characteristics:		
Composition.....	wheat with vermiculite overlay	wheat only
Dimensions (mm).....	{ wheat, 2.5 deep, 98 dia. vermiculite, 5 deep translucent	3 deep, 90 dia. translucent
Container.....		
Full-fed <i>Anagasta</i> larvae:		
Total number (in 505 days).....	6,433 (disease incidence low)	3,047 (diseased larvae/allotment decreased from 104 to none)
Daily average.....	11	6
Total per allotment.....	89	41
Natural enemies present:		
Type, number (generations).....	{ predator, 50 parasite, 20 intraspecific host competition, 505	predator, 50 predator, 505
Regulative factors, periods of dominance (days).....		
Parasitized larvae (per cent).....	75	..
Adult female host: parasite (ratio).....	1:7	..
Average number of mature predators: adult host.....	3	3.5
Wheat conserved (per cent).....	none	30

* Twenty-four allotments, one replaced weekly.

TABLE 4
DATA ON ECOSYSTEMS DEPICTED BY CORRESPONDINGLY
NUMBERED GRAPHS

Item	Ecosystem X*	Ecosystem XII*
Segment of ecosystem life:		
Began.....	June 25, 1964	Aug. 19, 1964
Years of life represented.....	7 and 8	6 and 7
Allotment characteristics:		
Composition.....	wheat only	wheat only
Dimensions (mm).....	14 deep, 44 dia.	14 deep, 44 dia.
Container.....	translucent	translucent
Full-fed <i>Anagasta</i> larvae:		
Total number (in 505 days).....	5,126 (disease highly variable/allotment)	4,062 (disease highly variable/allotment)
Daily average.....	10	8
Total per allotment.....	71	56
Natural enemies present:		
Type and number of generations.....	{ predator, 50 parasite, 20 predator, 75; intraspecific host competition, 430	predator, 50 { predator, 135; intraspecific host competition, 370
Regulative factors, periods of dominance (days).....		
Parasitized larvae (per cent).....	67.5	..
Adult female host: parasite (ratio).....	1:4	..
Average number of mature predators: adult host.....	2	3
Wheat conserved (per cent).....	5	6

* Twenty-four allotments, one replaced weekly.

TABLE 5
DATA ON ECOSYSTEMS DEPICTED BY CORRESPONDINGLY
NUMBERED GRAPHS

Item	Ecosystem XIII M ₁ *	Ecosystem XIVA*
Segment of ecosystem life:		
Began	Mar. 25, 1963	Aug. 10, 1964
Years of life represented	2 and 3	4 and 5
Allotment characteristics:		
Composition	wheat only	wheat only
Dimensions (mm)	10 deep, 50 dia.	8 deep, 58 dia.
Container	translucent	translucent
Full-fed <i>Anagasta</i> larvae:		
Total number (in 505 days)	{ 1,667 (nondiseased) 1,032 (diseased)	{ 2,115 (nondiseased) 260 (diseased)
Daily average	3	4
Total per allotment	46	58
Natural enemies present:		
Type, number of generations	{ predator, 50 parasite, 20 bacterium distributed by parasite, 505	{ predator, 50 parasite, 20
Regulative factors, periods of dominance (days)		parasite, 505
Parasitized larvae (per cent)	60	90
Adult female host: parasite (ratio)	1:3	1:20
Average number of mature predators: adult host	0.5	1
Wheat conserved (per cent)	22	24

* Twenty-four allotments, one replaced fortnightly.

TABLE 6
DATA ON ECOSYSTEMS DEPICTED BY CORRESPONDINGLY
NUMBERED GRAPHS

Item	Ecosystem I M ₂ *	Ecosystem XV†
Segment of ecosystem life:		
Began	May 20, 1961	Sept. 20, 1964
Years of life represented	5 and 6	2 and 3
Allotment characteristics:		
Composition	wheat only	wheat only
Dimensions (mm)	{ 4.5 deep, 73 dia. with 12-mm protective disc opaque	{ 4.5 deep, 73 dia. with 12-mm protective disc opaque
Container		
Full-fed <i>Anagasta</i> larva:		
Total number (in 505 days)	2,086 (nondiseased)	3,342 (disease incidence low)
Daily average	4	6
Total per allotment	58	46
Natural enemies present:		
Type, number of generations	parasite, 20	parasite, 20
Regulative factors, periods of dominance (days)	parasite, 505	parasite, 505
Parasitized larvae (per cent)	92.7	87.4
Adult female host: parasite (ratio)	1:24	1:13
Average number mature predators: adult host	(no record)	(no record)
Wheat conserved (per cent)	13	25

* Twenty-four allotments, one replaced fortnightly.

† Forty-eight allotments, two replaced fortnightly.

TABLE 7
MAXIMUM EFFICIENCIES OF PREDATOR, BACTERIUM, AND PARASITE
IN THREE ECOSYSTEMS

Item	Number of ecosystem and regulative agent:		
	VIIIB Predator	XIII M ₁ * Parasite- transmitted bacterium	XIV Parasite
<i>Anagasta</i> larvae			
(Full-fed):			
Total number.....	1,045	721	1,062
Number per day.....	3.6	2.6	4.0
(Diseased):			
Number per day.....	less than 1	3.7	less than 1
Female host-parasite (ratio).....	0:0	1:5	1:13
Minimum food conserved (per cent)†.....	30	21	25
Life of habitat allotment (weeks).....	24	48	48
Number of prey generations.....	4	8	8

* The 505-day period in the life of XIII M₁ (fig. 5) began 17 months after that depicted for XIII (fig. 7). The added *Anagasta* females indicated in fig. 7 initiated an entirely new *Anagasta* population that completely replaced the one destroyed by parasites.

† Approximate. Debris weight (40 grains) that remained in the average completely consumed allotment was subtracted from the separate weights of unconsumed allotments. The figures, therefore, became less accurate as the amount of unconsumed food increased. The weight of debris (not unused food) showed that the actual percentage of food conserved by regulative action may have been as much as 50 for VIIIB, 26 for XIII, and 37 for XIV.

TABLE 8
POPULATION COUNTS OF
TRIBOLIUM CONFUSUM, AND
BLATTISOCIUS, IN 24 HABITAT
ALLOTMENTS REMOVED FROM
DEFUNCT ECOSYSTEM XVIII
OCTOBER 11, 1966

Allotment age	<i>Tribolium confusum</i>		<i>Blattisocius</i>
	Adults	Larvae	
weeks	number	number	number
1.....	0	0	0
3.....	0	0	0
5.....	0	0	0
7.....	0	0	4
9.....	2	0	2
11.....	5	0	5
13.....	0	0	4
15.....	6	0	7
17.....	7	0	6
19.....	0	0	0
21.....	4	2	9
23.....	8	0	8
25.....	1	1	4
27.....	4	0	1
29.....	4	0	2
31.....	8	0	1
33.....	6	1	7
35.....	5	0	0
37.....	3	1	1
39.....	6	1	2
41.....	6	2	3
43.....	4	0	0
45.....	7	0	0
47.....	1	1	1
Total.....	87	9	67

TABLE 9

A COMPARISON OF HOMEOSTATIC CONDITIONS OF THREE SUCCESSIVE PERIODS OF TWO ABIOTICALLY IDENTICAL ECOSYSTEMS WITH PARASITE-REGULATED POPULATIONS*

Item	Successive periods in XXII:			Successive periods in XXIII:		
	305 days	100 days	100 days	305 days	100 days	100 days
Parasitization (per cent)	89.7	57	72.3	77.8	81.5	78.4
Female host: parasite	1:17.5	1:2.6	1:5.2	1:7.0	1:8.8	1:7.3
Number of adults emerging per day (average):						
<i>Anagasta</i>	1.2	0.9	1.3	2.2	0.76	0.76
<i>Devorgilla</i>	10.5	1.2	3.4	7.8	3.4	2.8
Weight of removed allotments (grains)	55	68†	80	53	57	81
Wheat conserved (per cent)	15.0	23.3	33.3	10.8	14.1	34.1
Number of <i>Tribolium</i> adults removed	5	107	58	0	1	3
Number of <i>Blattisocius</i> per <i>Anagasta</i> adults	scarce	scarce‡	scarce	scarce	scarce	scarce

* Each ecosystem contained 48 allotment habitats in translucent polystyrene plastic containers (habitat dimensions: depth, 9 mm; diameter, 56 mm.)

† The conservation of 11 grams of wheat per allotment during this 100-day period over that in XXIII is attributed to the predator action of approximately two *Tribolium* larvae per allotment.

‡ At the end of this period a temporary increase of *Tribolium* eggs resulted in an average of 2.3 *Blattisocius* (temporarily) for each of 18 *Anagasta* adults sampled.

The number of larvae that became full-fed per habitat allotment (120 grains of wheat) were 60 ± 5 , the maximum number that presumably would complete their development in the absence of natural enemies and of surplus larvae. Consequently, graphs II and IX may be compared with those exhibited in other ecosystems to show the relative effectiveness of prey-regulative natural enemies.

The significant lack of periodicity in the population fluctuation depicted in graphs II and IX was probably caused by the marked reduction of intraspecific competition by *Anagasta* larvae. If so, this competition could have been influenced, in turn, by (1) the random deposition of *Anagasta* eggs on the surface of the vermiculite layer, (2) the search made by the newly-hatched larvae through and beyond the vermiculite mass, and (3) the movement of partly developed larvae upward into the vermiculite mass. The somewhat greater variability in fluctuation amplitude shown in graph II compared with IX may result from the fewer partly grown larvae that became lost in the vermiculite mass.

This difference is indicated by the fact that about three to five dead, partly grown larvae were collected daily from the floor of IX. Such deaths never assumed significant proportions even in ecosystems in which the habitat allotments consisted, in part, of a vermiculite mass deeper than 11 mm—the number of larvae that became full-fed daily being between nine and ten.

Data from certain other ecosystems with habitat allotments of similar dimension, but lacking the overlay of vermiculite, indicated that if those in II had lacked vermiculite, the population fluctuations would have been as periodic as those depicted in graphs of X (fig. 4) and XIII M₂ (fig. 5); and that if those in IX (fig. 2) had lacked vermiculite, the parasite would have

annihilated its host and consequently itself.

So it appears that one function of an overlay of vermiculite, 7 mm or 33 mm deep, is to preclude cyclicity in fluctuation. However, this preclusion may not be complete if the vermiculite depth is shallow. Cyclicity is suggested in the graph of III (fig. 3). This graph represents a population regulated by intraspecific competition of *Anagasta* larvae, an effect of an overlay of vermiculite 5 mm in depth. In this ecosystem, few, if any, larvae died after developing through the first instar.

In the population represented by the graph of III (fig. 3) an average of 11 larvae became full-fed per day (table 3). This unusually high average, however, was an effect of parasitization (75 per cent) causing precocious maturity of parasite-inhabited larvae, thereby indirectly increasing the larval host population (Flanders and Badgley, 1960). Although the parasite population was nonhost-regulative (Flanders and Badgley, 1963) with female host-parasite ratio at 1:7, the annual production of adult parasites was greater than in any other of the ecosystems.

The effect of nonregulative parasitization on increasing the amplitudes of population fluctuation is shown by comparing the graphs and tables of X and XII (fig. 4, table 4).

The graph of XVII (fig. 3) represents a population regulated by the predator aided by (1) the shallow depth of the habitat allotment, (2) the lack of a vermiculite overlay, and (3) the absence of the parasite. This graph and that of III (fig. 3) represent contrasting extremes in the equilibrium positions of the populations. Note the average nadir levels of oscillation in both graphs. In XVII with a low equilibrium position, 30 per cent of the wheat was conserved. In III with its high position, no wheat was conserved. During the most effective prey-regulative

period, the XVII population fluctuations lost their periodicity, presumably because interneecine larval strife was low or absent.

The gradual increase in the degree of prey-regulation in XVII was followed by a sharp decrease. The decrease in prey-regulation, however, was so greatly prolonged that the proportion of conserved wheat decreased by about 20 per cent. This failure of the predator to resume maximum control of the prey within six months was correlated with an excessive accumulation of *Anagasta* spoor (Flanders and Badgley, 1963). However, it is significant that when the translucent containers, 90 mm in diameter, were replaced by opaque ones, 73 mm in diameter, control by the predator was readily reestablished.

The graphs of X and XII (fig. 4) represent populations regulated for the most part by wheat depletion. The marked periodicity of these populations presumably was caused by the concentration of the *Anagasta* eggs on certain allotments rather than their random distribution through each ecosystem, so that interneecine strife between the newly hatched and the feeding larvae was accentuated. This presumption also holds for the initiation of fluctuation cyclicity in XIII (fig. 5) where interneecine competition occurred between feeding larvae which, for the most part, died of disease (Flanders and Hall, 1965).

The high fluctuation amplitudes characterizing the population in X was caused by the 67.5 per cent parasitization which, in turn, produced the unusually high number (71) of full-fed mature larvae per habitat allotment. The number per habitat allotment in XII (table 4) where there were no parasites, was 56. The smaller number of larvae consumed about the same amount of wheat as did the larger number. Note that the average number of larvae that became full-fed per habitat

allotment in XIVA (table 5), where the parasite was highly host-regulative, is 58. Since 90 per cent of these were parasitized, they consumed a much smaller amount of food than did those in XII, where the average number of larvae per allotment was 56.

Graphs of XIII M₁ and XIVA (fig. 5) represent *Anagasta* populations regulated at low densities directly and indirectly by *Devorgilla* through its transmission of *Bacillus*. Because of these low densities, habitat allotments were replaced after 48 weeks, instead of 24. Even then, the 22 to 24 per cent of food conserved represented better control than that by *Blattisocius* in XVII (fig. 3), despite the possibility of twice as many *Anagasta* generations per habitat allotment caused by the doubled exposure time.

Ecosystems II and V established in 1957 were combined in October, 1963, to form II plus V (fig. 7). Thereafter, each of the habitat allotment replacements consisted entirely of wheat 6.5 mm deep and 68 mm in diameter. As a consequence of the doubled number of habitat allotments and the decreased depth of each, the parasite became host-regulative. Twenty-eight per cent of the wheat supply was conserved instead of none, as occurred previously with the two 24-unit ecosystems. The average number of full-fed larvae per allotment decreased from 65 to 50. For the period under consideration (fig. 7), a wheat depth of 6.5 mm served as a host-protection threshold.

The marked differences in the frequencies and the amplitudes of the fluctuations depicted by the graphs of XII (fig. 4) and XIVA (fig. 5) derive from the various host-regulative factors. The similarities of those of X and XII (fig. 4) reflect the relatively large population and associated mortality of the early stages of *Anagasta*.

The markedly reduced amplitudes of certain oscillations in the graph of para-

site-free XII are probably an effect of increased predation.

That the predator-parasite cooperation in X (fig. 4) was slightly host-regulative is indicated by the maintenance of minima populations at average nadir densities one-half those in XII, where the parasite was absent.

Parasite, predator, and bacterium were present in both XIII and XIVA (fig. 5); in both, predator action during the period under consideration was negligible, averaging one adult or less per adult *Anagasta*. In XIVA, bacterial action was negligible; it destroyed only about 11 per cent of the feeding larvae.

In XIII about 40 per cent of the larval mortality was caused by the bacterium and about 60 per cent by the parasite. However, since the female host-parasite ratio was only 1:3, it was evident that the parasite itself was not regulative. Instead, host regulation was an effect of the bacterium aided by the parasite.

It is probable that should the host population have been released from regulation by bacterium-parasite cooperation for a period long enough to allow the predators to increase, regulation would have occurred through predator-parasite cooperation (Flanders and Badgley, 1963).

Although the bacterium was present in XIVA, the female host-parasite ratio of 1:20 showed host regulation to be an effect of the parasite's host-finding efficiency. An average of about 20 parasites was necessary to destroy the surplus *Anagasta* larvae, that is, the number in excess of the number of parents.

Intraspecific competition by *Anagasta* larvae was probably almost absent in XIVA (table 7), because chronologically they were distributed fairly evenly and their densities were very low. In XIII M₁ (fig. 7, table 7), on the contrary, such competition was probably very intense during certain periods and consequently responsible for the marked

cyclicality of the fluctuations. The number of diseased larvae in XIII M₁ and XIVA were observed in 20 replaced allotments in each (see table 2, page 347, Flanders and Hall, 1965).

The graphs of I M₂ and XV (fig. 6) represent populations generally regulated by parasites at low densities. Owing to the conservation of food, habitat allotments in both I M₂ and XV were replaced at the end of 48 weeks instead of 24. However, subsequently I M₂ was parasitically annihilated. This took place at the end of October, 1963, after a sequence of 30 allotments had not been replaced until each was two years old.

Twice the size of I M₂, XV was established to insure the mating of *Anagasta* and thus preclude its annihilation at low parasite-determined equilibrium positions. Although the number of habitat allotments in XV was 48, double the number in I M₂, and occupied double the space, the increase in the population of full-fed *Anagasta* larvae was not proportional, presumably because of the greater surface area subject to search by the parasite. The increased total surface area of the habitat allotments apparently reduced parasite-searching efficiency and led to (1) a decrease in the average number of full-fed larvae per allotment from 58 to 46 and (2) a female host-parasite ratio of 1:13 instead of an expected 1:24. The greater numbers of *Anagasta* adults and consequent egg production tended to preclude annihilation of *Blattisocius* by starvation. The decrease of about 20 per cent in the number of full-fed larvae per habitat allotment was correlated with about 50 per cent increase in the amount of food conserved per allotment. This also occurred in II and V (fig. 7). The 1:13 ratio lasted only through June, 1966. Thereafter, for another 505-day period the female host-parasite ratio was 1:23, a ratio always correlated with the disappearance of *Blattisocius*.

However, the doubling of the food supply in order to insure the synchronous emergence of *Anagasta* males and females failed. Parasitic annihilation of the *Anagasta* population in XV occurred during November and December 1967, a period in which nine *Anagasta* adults emerged at intervals of such length as to preclude mating.

A comparison of the maximum effi-

encies of the regulative agents of *Anagasta* populations for 275-day periods in 1965 and 1966 is shown in table 7.

It is apparent that the *Anagasta* ecosystems tend to exhibit oscillations in population density despite the constant availability of food (the ultimate limiting factor), the food being supplied in quantities that are entirely independent of reproductive activities.

PERIODICITY AND TERRITORIALITY

In the *Anagasta* ecosystems the larval populations rarely "overshoot" their food supply because of the "territoriality" of the feeding stages. Unlike the blowfly populations studied by Nicholson (1954), the number of larvae per unit of food supply rarely increases so much that the number becoming adult decreases.

Population fluctuations, as observed to date in the *Anagasta* ecosystems in which natural enemies are present but not prey-regulative, appear to be based on fluctuations inherently effected by the intraspecific competition of the *Anagasta* larvae.

Periodicity of such fluctuations may be accentuated by the host's shorter reproductive period relative to the period of its development. In any case, the relative numerical relations of host and parasite densities alone (DeBach and Smith, 1947) do not sufficiently explain population cyclicity.

Periodicity of *Anagasta* increase and decrease appeared to be caused by variations in the intensity of the intraspecific competition of (1) the newly hatched larvae for space, of (2) the feeding larvae for the wheat, and of (3) the predator for its prey (Flanders and Badgley, 1963).

Rates of food consumption under physically uniform environments depend, of course, on the age distribution of the population, particularly the pro-

portion of feeding larvae. For the populations represented by graphs (figs. 1 to 6), the average number of larvae that became full-fed per day and the average number of full-fed larvae that developed per allotment habitat are shown in tables 1 to 6 inclusive.

The cyclic nature of the population's equilibrium position and the occurrence of these larvae are not clearly apparent when population graphs are based on monthly summations of the daily mortality of adults. Such graphs were used by Flanders and Badgley (1963), because they accentuated the different fluctuation characteristics of populations regulated by different agents.

The cyclic nature of *Anagasta* populations in balance with their food supply, as in X and XII (fig. 4), became clear when the population graphs were based on five-day summations of adult mortality—that is, when the summations used are one-tenth of the generation instead of six-tenths. However, in ecosystems where populations are well-regulated by a parasite or a predator, cyclic fluctuations may occur, but they are not so well marked. This is apparent in I (fig. 6) and XIVA (fig. 5).

All but three of the 12 graphs (figs. 1 through 6) that represent the populations of full-fed larvae in 12 ecosystems show distinct cyclicity with the periods equal to the average life cycle of *Anagasta*. It seems logical to assume that

such periodicity was established automatically because of variations in the intensity of internecine strife by newly hatched and feeding larvae. Once variability in internecine strife is initiated it tends to become accentuated until a maximum is attained that is commensurate with the amount of available food and the portion of the life cycle to which intraspecific strife is limited. The egg-to-egg period of *Anagasta* establishes the cyclic nature of the fluctuations in the overlapping larval populations, this being stabilized by territorial fighting and starvation, an activity of the newly hatched and growing larvae.

Anagasta ecosystems have demonstrated that this "territory action" permits populations to survive, to perpetuate themselves, and to attain equilibrium positions.

Territory action was one of the three principal extrinsic mortality factors listed by Flanders and Badgley (p. 155, 1963) that tend to eliminate, before feeding, the surplus larval progeny of each generation.

When the surface diameter of a habitat allotment is increased from 44 mm to 70 mm, and from 25 mm to 90 mm, internecine mortality is reduced so that wheat consumption is hastened by a month or more.

When the diameters of the habitat allotments are 25 mm or less, internecine strife of partly developed *Anagasta* larvae occasionally may be so severe that relatively large numbers migrate from their habitats and ultimately starve. This apparently occurred with 26 fully utilized habitat allotments (25 mm \times 42 mm) in parasite-free XVI. The total number of adult *Anagasta* from each of these nearly disease-free allotments averaged only 43, instead of over 60.

It is significant that the low rates of wheat consumption in habitat allotments of different dimensions were reversed, when similar allotments arbitrarily received excessive numbers

(1,000 \pm) of newly hatched larvae as did the habitat allotment shown in figure 11. With such excessive numbers, territory action, if any, was not apparent.

Repeated tests (figs. 12 and 13), however, showed that *Anagasta* larvae may exhibit marked territoriality. When 1,000 newly hatched larvae were provided with relatively few isolated flakes of wheat (3 mm to 6 mm in diameter) from one to ten lodged themselves under each flake. The first arrivals fastened the flakes to the substrate, some enclosing themselves singly in cocoons (fig. 14). Larvae that subsequently contacted the isolated flakes were either forced to move on or were killed in conflict. In one instance (fig. 12) up to 10 larvae found refuge under each flake, the rest moved out of the immediate area. The larvae tended to remain under these flakes, and during the first three weeks they consumed relatively small portions of each. They appeared reluctant either to leave the protective cover or to consume it. However, through aggressive territorial action, the number per flake gradually diminished until at the end of three weeks the average was less than one. This was readily observed under the microscope, since the larvae firmly fastened the flakes to glass substrates.

If at any time during the three-week period the flakes were covered with a layer of vermiculite several millimeters in depth, all the larvae moved away from the flakes within 24 hours in search of more abundant food. This indicates that newly hatched larvae respond first to their need for shelter.

With excessive numbers of newly hatched larvae, food distribution determines (1) population pressure, (2) the degree of territory action, and (3) the proportion of food consumed in a given period (figs. 11 and 12). Territory action may be the key factor that determines the cyclic nature of *Anagasta* population fluctuations (X, XII, and XIII M₁, figs. 4 and 5). This would be

the case if certain instars, such as the third or fourth, would establish territory that would exclude early instars. Territory action, however, appears to be of little, if any, importance in affecting population fluctuations when newly hatched larvae have difficulty in locating the food supply as in IX (fig. 2); or when the prey-regulative action of natural enemies tends to reduce the number of contacts between early larval instars to zero, as in XIVA (fig. 5).

Two types of *Anagasta* populations lack cyclic fluctuations: one in which the newly hatched larvae are relatively scarce but can contact food immediately (XVII, fig. 3 and XIVA, fig. 5), and one in which they are abundant but forced to search a relatively large area for food (IX, fig. 2). Thus the distinct cyclic fluctuations apparently occurred only when a relatively high density of newly hatched larvae did not need to search for food, and internecine strife occurred immediately upon hatching. As pointed out by Flanders and Badgley (1963), relatively few of the larvae that had commenced to feed and to develop died of starvation.

Similar cyclic fluctuations with periods generally equal to the average life cycle of the species were observed by Takahashi (1963) with the moth, *Ephestia cautella* Walker.

The intensity of the internecine mortality of newly hatched and feeding larvae is, of course, a function of the relative number of eggs. The effect of egg production on population fluctua-

tions of *Anagasta* was strikingly evident in I M₂ (fig. 9), after a continuous aramite application that depressed *Blattisocius* reproduction.

As noted above, population fluctuations tend to be noncyclic when the newly hatched larvae either rarely come in contact with each other because of their scarcity (XV or XVII) or they must search for food by dispersing through vermiculite (II and IX). In II and IX (figs. 2, 3, and 6), the fluctuations are irregular, more frequent, and lower in amplitude. Although the equilibrium positions of the full-fed larval populations in IX (fig. 2) and X (fig. 4) are practically the same (determined by the constant amounts of food), their fluctuation amplitudes are markedly different, one having vermiculite overlying the wheat. This provides an exception to Smith's (1935) idea that the average density of a population may influence the amplitudes of its oscillations.

The fluctuation amplitudes of parasitized populations that are not, however, parasite-regulated are higher than those of parasite-free populations (X and XII, fig. 4). This appears to be an effect of differences in the average densities of such populations and supports Smith's (1935) concept that the average density may influence the amplitudes of oscillations.

The separate growth curves of host and of parasite in IX (fig. 8) for a period of ten host generations show that the parasite curve lagged behind that of the host by 10 to 15 days.

SUMMARY

An *Anagasta* population possesses an inherent capacity to adjust its abundance to the capacity of the environment. When the food supply is constant, such an adjustment may not involve cyclic fluctuations about an average density, either in the absence or in the presence of natural enemies, provided

that the latter are able to maintain such a low average host density that internecine strife between newly hatched and feeding larvae is precluded. The *Anagasta* population in XIII (fig. 5) is remarkable for its periodicity when the steady density of the full-fed larvae is very low. This is correlated with a large

number of immature larvae needed to support the disease organism.

With *Anagasta* populations, the higher fluctuation amplitudes of parasitized, but wheat-limited, populations relative to those of unparasitized, but wheat-limited, populations appears to be an effect of the precocious maturity of parasitized larvae. This precocious maturity permits three parasitized larvae to become full-fed on the amount of wheat needed to enable two unparasitized larvae to become full-fed (Flanders and Badgley, 1960).

For each stabilized ecosystem as a whole, excepting II and IX (table 2), the oscillations of host and natural enemy populations tend to coincide, regardless of whether or not the latter are host-regulative (fig. 7).

Oscillation of the population of full-fed larvae may be modified to some extent by the replacement of adult *Anagasta* by adult *Devorgilla*, with the consequent reduction in number of newly hatched larvae and larval strife. The relatively short life cycle or high reproduction rate of the parasite may be responsible for the generally low amplitudes and the irregular periods of fluctuation that appear to characterize parasite-regulated populations (Smith, 1937).

The graph for I (fig. 1) shows a gradual decrease in the full-fed larval population and an increasing irregularity of fluctuation. Allotment habitats were 14 mm deep, and the containers were opaque. The decrease in equilibrium position was attributed to the increasing effectiveness of parasite-predator cooperation and regulation. That the host-searching by the predator is more successful in opaque containers is evident when the graph of I (fig. 1) is compared to that of X (fig. 4). The parasite-predator cooperation that occurred in X was not generally prey-regulative. However, it reduced the average nadir densities of

the full-fed larval population of *Anagasta* to one-half of that in the equivalent XII, in which there were no parasites.

The graphs for III (fig. 3) and II and IX (fig. 2) depict the irregular periodicity that was characteristic of *Anagasta* ecosystems in which the upper portion of the allotment habitats consisted of vermiculite. Allotment habitats were 7.5 mm, 18 mm, and 36 mm deep, respectively, and all containers were translucent. The fluctuation amplitudes decreased with the increase of vermiculite depth. This was correlated with the increased time spent in searching by the newly hatched larvae. An average of nine larvae was full-fed daily in II and IX. In III, effect of parasitization on larval development permitted the number to increase to 11.

The graph for X (fig. 4) depicts regular fluctuations that were remarkable for their extreme amplitudes as well as for their periodicity. Allotment habitats were 14 mm deep, and the containers were translucent. The regularity of fluctuation frequencies and amplitudes was an indirect effect of host-nonregulative parasitization (nonreciprocal balance). The equilibrium position density was increased by the parasite-induced increase in the number of full-fed larvae. Periodicity was enhanced when adult parasites were substituted for adult hosts during the 20-day nadir of each oscillation, so that the number of eggs then deposited was extremely low.

The graph for parasite-free XII (fig. 4) depicts cyclic fluctuations of less extreme amplitudes and of less regularity than the graph for X, despite similar allotment habitats and containers. An average of eight larvae became full-fed daily in XII, 10 in X. Apparently, the lower average was an effect of predator regulation for 135 days following the highest peak in host-egg production.

The graphs for XVII (fig. 3), XIII

M₁ and XIVA (fig. 5) depict fluctuations at the lowest levels of equilibrium. Allotment habitats were 3, 10, and 8 mm deep, respectively. Six, three, and four larvae became full-fed daily. The host-regulator was the predator in XVII, parasitic transmission of *Bacillus* sp. in XIII M₁ (Flanders and Hall, 1965), and the parasite in XIVA—each, under the circumstances, exhibiting reciprocal balance.

The marked periodicity and relatively uniform amplitudes of the oscillations depicted for XIII M₁ (fig. 5) were caused when adult parasites were substituted for adult hosts during the 30-day nadir of each oscillation. The unusually long and uniform periods of low egg production and the low amplitudes of the uniform fluctuations appeared to be an effect of the low equilibrium position resulting from the destruction of about one-third of the larvae by disease. Otherwise, more larvae would have become full-fed and would have yielded enough adult *Anagasta* to shorten the periods of low egg production. Compare the long periods of time that oscillations of XIII M₁ remained at nadir positions to the short periods of time that oscillations of X (fig. 4) in which disease was negligible were at nadir positions.

The data show that:

(1) The predator in the absence of the parasite is almost continuously prey-regulative in ecosystems in which allotment habitats are 10 mm deep or less and consist entirely of wheat flakes (VIIIB and XVII).

The overall predator-prey ratio in IX with its 33-mm cover of vermiculite was as high as in vermiculite-free ecosystems in which the predator was prey-regulative (see tables 2 and 3). This indicates that predator action was largely limited to the surface area of the vermiculite cover. The prey-mortality thus caused merely replaced that which would have occurred anyway, either by failure of

the prey larvae to find the wheat supply, or by their internecine action. Also, prey regulation in vermiculite-free ecosystems probably depends on egg destruction by predators supplemented by territorial action among larval prey.

(2) When the depths of the allotment habitat are between 10 mm and 30 mm deep, and the containers are opaque (I and IV, fig. 1), predator-parasite cooperation appears to be most effectively host-regulative. The predator is never prey-regulative when the allotment habitats in translucent containers consist in part of vermiculite (II, fig. 2; III, fig. 3; and IX, fig. 2) and is prey-regulative for only half the time when the depth of the allotment habitat exceeds 10 mm, and parasites are absent (XII). Prey-regulation is minimum in X (fig. 4), which is a duplicate of XII (fig. 4), except that parasites are present.

(3) Population equilibria, regardless of the type of regulative agents, are characterized by associated prey and natural enemy fluctuations. However, in ecosystems in which the *Anagasta* equilibrium position is parasite-determined, each growth curve of the host population begins several days after that of the parasite; the emergence of the adult parasite presaging that of the adult host.

(4) The fluctuations in *Anagasta* reproduction, generation after generation, are cyclic, regardless of any prey-regulative action by natural enemies, provided that newly hatched *Anagasta* larvae do not need to search for food.

The periodicity of the cycles equals the generation time of *Anagasta*, presumably because of the inherent variations in mortality caused by the internecine strife among newly hatched larvae.

(5) The fluctuations of *Anagasta* reproduction become noncyclic when mortality from internecine strife is largely replaced by mortality caused by the

necessity for the newly hatched larvae to search through and beyond a mass of nonnutrient material, such as vermiculite (fig. 2). Nonecyclic fluctuations appear to be the effect of chance variations in food finding. It is significant that the complete food-utilization period is prolonged, as the volume of the nonnutrient zone is increased (Flanders and Badgley, 1963).

(6) Prey-regulation is attained when the natural enemy finds its prey becoming scarce and difficult to find—and when the relative densities of the two populations (within a generation time of the host) are such that the chance for host and its natural enemy to be at the same place at the same time approaches zero. For prey regulation, it is not necessary for the distances separating the prey individuals to be greater than the range of the natural enemy, as postulated by DeBach and Smith (1941).

(7) Wheat is conserved in *Anagasta* ecosystems when the density of the wheat-eating population is regulated by natural enemies. Differences in the amount of wheat consumed, however, may be markedly influenced by changes in the prey-finding capacity of the natural enemy.

Prey regulation by the predator occurs when the rate at which an allotment of wheat is completely consumed requires up to 300 days, instead of 60 day (when natural enemies are ineffective). Prey regulation by the parasite precludes complete wheat consumption in any allotment. The prey in an eco-

system is annihilated when it so reduces the wheat depth that none escape parasitic attack. Such an annihilation occurred with I M₂ when the wheat allotments were replaced only after each was 500 days old.

This differential in prey regulation by natural enemies tends to depend on the decreasing capacity of the predator to find its prey (XVII, fig. 3) and the increasing parasite population as more wheat is consumed. Both tendencies apparently derive from the prey's preference for ovipositing in the more highly infested wheat allotments (Flanders and Badgley, 1963). In both cases the conserved wheat may become populated by relatively high numbers of prey. However, since prey searching by the predator is not limited to the conserved wheat, and whereas prey searching by the parasite is largely so limited, predator action is usually much less efficient than parasite action.

(8) Each ecosystem population (10 generations or more) has a characteristic ratio of natural enemy adults to host adults, regardless of the regulating factor. In ecosystems in which the equilibrium positions are determined by enemy action (dependent on host density), the proportion of enemy adults is greater than it would be otherwise. This proportion increases as the average host density decreases. If an ecosystem is properly established, the natural enemies (parasites) do not become numerous enough to annihilate it.

CONCLUSIONS

Relative to the size of their organisms, the *Anagasta* ecosystems discussed in this report are not so small that potential evolutionary relationships are absent, nor is prey capture so easy that coaction of the different species is disoperative (Huffaker, 1958).

The prolificacy of a natural enemy

species, although dependent on prey finding, has little bearing on the equilibrium position. Instead, prolificacy is determined largely by the environment (Smith, 1929). Variations in the species' reproductive rate affect only the time necessary for the species to fill the environment to capacity; they do

not influence that capacity. The population capacity of certain of the *Anagasta* ecosystems is determined by prey-regulative natural enemies.

Anagasta ecosystems demonstrate Smith's (1939) concept that although many natural enemies thrive only when the prey population is dense, others thrive when the prey is scarce; that the true measure of the prey-regulative capacity of a natural enemy is its efficiency when the density of prey population is low.

Fluctuations and their frequencies and amplitudes that characterize the various populations of the *Anagasta* ecosystems—appear to depend primarily on the intraspecific competition of the prey population. The regularity of the fluctuations of *Anagasta* populations in the laboratory supports Muir (1914) and Solomon (1949): that population fluctuations of a given ecosystem exhibit a characteristic pattern, if the physical characteristics of the environment are relatively constant.

Some of the principles illustrated are as follows:

(1) Fortuitous lifetime protection of the prey from attack by natural enemies is prerequisite to regulative action.

Regulative action by the natural enemy occurs when prey protection is at or near its threshold; prey is annihilated when protection decreases below

the threshold. As protection increases above the prey-regulative threshold and the prey population increases, so also does the natural enemy.

(2) The prey-regulative capacity of a natural enemy is a function of (a) prey distribution and (b) the searching pattern of the natural enemy.

Efficiency of the natural enemy is indicated by the ratio of adult female natural enemies to one adult female prey. When food for the prey is constant in availability and quality, the amount conserved during a period of about 10 generations of the prey is the measure of natural enemy efficiency. Population abundance is in itself not a measure of population regulation. Prey regulation by one agent is precluded by an agent of greater efficiency.

(3) The equilibrium positions of the population vary directly with the regulative efficiency of the responsible agent.

Population fluctuations around an equilibrium position are inherent in prey-predator interactions. If such fluctuations are based on the intraspecific competition (territoriality) of the prey, they may exhibit periodicity in fluctuations.

(4) Replacement of a prey-regulative general predator by a prey-regulative specific parasite permits the establishment of organisms that compete with the prey.

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