Chapter 9
POPULATION DYNAMICS
GENERAL CONSIDERATIONS

I. Insect Populations and Population Dynamics.

A. Definition of Population: a collective group of individuals of the same species occupying a particular space.

B. Populations may be divided into demes. A deme is a smaller unit of a population found in a localized area. Demography is the study of the vital statistics of a population.

C. Definition of Population Dynamics: that aspect of population ecology dealing with forces affecting changes in population densities or affecting the form of population growth.

D. Populations have 2 basic requirements:

1. They have a minimum size; and
2. They occupy an area containing all needed resources.

E. Once the above requirements are met, one can estimate the following "statistical" attributes:

1. Natality (birth rates)
2. Mortality (death rates)
3. Age distribution
4. Sex ratios

F. A population of organisms may display:

1. Growth
2. Dispersion
3. Genetic variability
4. Continuity in time.

G. Populations are not isolated entities, but exist in "communities" with other populations of species.

II. Communities

A. Communities are associations of different species which are relatively consistent associations and are classified based upon the major plant species within the community (i.e., Oak-Hickory forest, Tropical Rain forest).

B. Trophic levels or nutritional associations can be distinguished between interacting species. These different levels are referred to as:

1. Primary producers (green plants)
2. Primary consumers (herbivores)
3. Secondary consumers (carnivores)
4. Decomposers
5. Scavengers

C. Definite food chains can be distinguished in the community. Branching food chains make up food webs.

1. Food chain: a trophic path or succession of populations through which energy flows in an ecosystem as a result of consumer consumed relationships.
2. Food web: a complex of branching, joining, or diverging food chains that connect together the various populations in an ecosystem.

D. Communities exist within "ecosystems".

III. Ecosystems

A. An "ecosystem" is an interacting, self-sustaining, natural system of living organisms (the community) and of a chemical-physical component (the abiotic environment). This is the basic functional unit in ecology.
B. In biological control, we deal with "agroecosystems" which are ecosystems composed of cultivated land, the plants contained or grown thereon, and the animals associated with these plants. These are extremely limited systems and they can be very unstable.
C. Within ecosystems, populations are thought to exist in a state of "homeostasis". This idea was suggested by Herbert Spencer (1897). Homeostasis is the tendency of a system to maintain a dynamic equilibrium, and if disturbed, to restore that equilibrium. The more complex a biological system (community) the more stable it usually is to disturbances. The more complicated the system the more reliable is the system of checks and balances against rise and fall.

IV. Arthropod Pest Populations Within Agroecosystems.

A. In agroecosystems one strives to maintain arthropod pests at non economic levels (not a "pest free" situation).
B. Economic Injury Level: the level at which insect induced damage can no longer be tolerated and therefore the level at or before which it is desirable to initiate deliberate control activities.
C. Economic Threshold: the pest density at which control measures should be applied to prevent an increasing pest population from reaching the economic injury level.
D. Economic threshold may also be referred to as the "action threshold", "density treatment level" or "treatment threshold". These terms usually do not include the influence of market values on the system and mainly refer to the impact of the pest upon the plant's productivity.
E. Most insects are maintained at very low population levels by "natural control" and are not viewed as pest species. Only 10,000 to 30,000 of the one million insect species known are pests. These pests feed on crops, forests, pasture lands, or livestock , comfort or possessions.
F. Natural control is the maintenance of a more or less fluctuating population density within certain definable upper and lower limits over a period of time by the combined actions of the whole environment.

V. Population Growth and Regulation

A. Population ecology was originally confined to demography of human populations as was practiced by Chinese and Egyptian census takers.
B. Malthus (1803) published "Essay on the Principles of Population" which considered overpopulation of mankind. His ideas were similar to those of Giovanni Botero (1588) who proposed the same concept of population regulation.
C. Malthus' idea was that "Man" increases at a geometric rate but his food supply does not. Soon became known as the "Malthusian Principle". Malthus was criticized because "Man" was considered to be capable of controlling his own birthrate. Another problem was that he considered the increase in subsistence (food & housing) was in a arithmetic ratio which was a major error. If this was so populations would increase without limit.
D. Charles Darwin (1859) accepted Malthus' principle. He placed much stress on:
1. Biotic mortality factors in the environment;
2. Competition as a major regulation factor; and
3. Climate as a factor in limiting population growth.

E. Herbert Spencer (1897) emphasized the concept of stability of the heterogeneous state and the instability of the homogeneous state.

F. Harry Scott Smith (1929) argued that the introduction of a complex of natural enemies (rather than a single species) should be employed in classical BC programs. He emphasized that the different kinds of natural enemies available vary as to the particular habitats where they excel and that the biological control to be expected from their combined actions, as conditions vary from place to place and time to time, would be greater than that to be expected from the action of any one of them alone.

DEFINITIONS OF POPULATION ECOLOGY TERMS

Abiotic mortality factors: *Non-living environmental factors that bring about premature death of plants and animals.*

Agroecosystem: *The ecosystem composed of cultivated land, the plants contained or grown thereon, and the animals associated with these plants.*

Area of discovery: *A variable equal to the width of track along which a female parasite searches multiplied by the length of the track accumulated while searching through the parasite's lifetime. Fluctuates with parasite density due to "interference". Abbreviated "a".*

Biotic mortality factors: *Living environmental factors that bring about premature death of plants and animals.*

Carrying capacity: *The density level at which the rate of increase of a species population is zero which is equivalent to the equilibrium population density. Abbreviated "K".*

Competitive exclusion principle: *If two species are similar enough to each other in their requirements (or niches), then one will go to extinction due to competition in the areas where their population distributions overlap. Also known as Gause's Principle, Grinnell's Axiom, Volterra-Gause Principle, and Competitive Displacement Principle.*

Conditioning forces: *Environmental factors or agents which, uninfluenced by density, contribute to the setting or fixing of a framework of potential environmental capacity or affect interim population realization when capacity is not attained.*

Deme: *A smaller unit of a population found in a localized area.*

Delayed density-dependent mortality: *Mortality inflicted on the members of a population, the magnitude of which is determined by the density of the population at some time in the past.*

Density-dependent mortality = Facultative mortality: *Mortality inflicted on the members of a population, the degree of which is related to or affected by the density of the population.*

Density-independent mortality = Catastrophic mortality: *Mortality inflicted on the members of a population, the degree of which is unrelated to or unaffected by the density of the population.*

Direct density-dependent mortality: *Mortality inflicted on the members of a population, the magnitude of which increases as the current density of the population increases and which decreases promptly as the current density of the population declines.*

Economic injury level: *The pest population density level at which insect induced damage can no longer be tolerated and therefore the level at or before which it is desirable to initiate deliberate control activities. Abbreviated "EIL".*

Economic threshold: *The pest population density at which control measures should be applied to prevent an increasing pest population from reaching the economic injury level. Abbreviated "ET".*

Ecological homologues: *A species which has the same niche as another species. The two species do not have to be related genetically.*

Ecosystem: *An interacting, self-sustaining, natural system consisting of living organisms (the community) and of a chemical-physical component; the basic functional unit in ecology.*

Environmental capacity: *The level of population for a species which an environment can sustain without permanent change.*

Exponential growth: *The tendency for populations to grow in numbers according to a geometric progression.*

Food chain: *A trophic path or succession of populations through which energy flows in an ecosystem as a result of consumer/consumed relationships.*

Food web: *A complex of branching, joining, or diverging food chains that connect together the various populations in an ecosystem.*

Functional response: *The changes in the number of attacks per parasite (or predator) upon the host as the host (or prey) density changes. Inversely density-dependent.*

Genetic feedback: *Theory of population regulation based on the continued genetic change of a host and its parasite through time.*

Governing mechanism: *The actions of repressive environmental factors, collectively or singly, which intensify as the population density increases and relax as this density falls (= density-dependent action).*

Handling time: *The time interval that elapses from the first encounter of a host (or prey) by a natural enemy until the instant when the natural enemy resumes its search.*

Homeostasis: *The tendency of a system to maintain a dynamic equilibrium and, if disturbed, to restore that equilibrium. Also termed* population equilibrium *or* population balance.

Hypervolume model of niche: *Technique used to describe niche of a species using several variables such as temperature, humidity, food preferences, etc.*

Interference: *A form of intraspecific competition between individual natural enemies at high natural enemy densities. Refers to interruptions in searching experienced by chance meetings of parasites.*

Intrinsic rate of increase: *The fraction by which a population increases in size per unit of time. Abbreviated "r".*

Inverse density-dependent mortality: *Mortality inflicted on the members of a population, the magnitude of which decreases as the current density of the population increases and which increases as the current density of the population decreases.*

Killing value: *Percentage mortality due to some agent expressed in logarithms to the base 10. Abbreviated "K" factor.*

Logistic growth: *The combination of the tendency for populations of organisms to grow in numbers according to a geometric progression, and the tendency for the environment to inhibit the attainment of excessively high densities by such growing populations.*

Natural control: *The maintenance of a more or less fluctuating population density within certain definable upper and lower limits over a period of time by the combined actions of the whole environment.*

Niche: *The place or position, in both a physical and a functional sense, of a species population in an ecosystem as determined by the full complex of environmental factors impinging on and limiting the population.*

Nicholsonian parasite: *A parasite which produces mortality in its host in a delayed density-dependent manner.*

Nonreciprocal density-dependent mortality: *Mortality inflicted on a population by a biotic mortality factor whose own numbers are not changed as a consequence.*

Numerical response: *The increase in parasites or predators as a result of the increase in their host or prey, respectively.*

Population: *A collective group of individuals of the same species occupying a particular space.*

Quest constant: *The value of the "area of discovery" when the natural enemy density is equal to one individual per unit area (i.e., 1 parasite per cm2).*

Reciprocal density-dependent mortality: *Mortality inflicted on a population by a biotic mortality factor whose own numbers are changed as a consequence.*

Steady state: *Condition in which parasite and its host coexist in a state of equilibrium.*
Volterra's principle: *If two species (predator/prey, parasite/host) are destroyed at the same rate by some outside agency (such as a pesticide application), the prey will proportionately increase and the predators will proportionately decrease.*

Chapter 10
DENSITY INDEPENDENT MORTALITY FACTORS AND THEORIES OF POPULATION REGULATION

I. Density Independent Mortality Factors

Density independent factors determine population changes and set the stage for the existence of populations. Density dependent factors are primarily responsible for regulating populations about an average level of abundance.

II. Abiotic Factors include such things as Temperature, Humidity, Rainfall, Soil pH, etc.

A. General effects of weather on populations include:

1. Insects blown up to snow covered mountain peaks;
2. Heavy rains that reduce insect populations;
3. Winds that carry migrating insects out to sea; and
4. Increases in humidity which produces conditions suitable for Epizootics in populations.

III. Effects of Temperature on Development

A. Developmental times decrease with increases in the temperature and developmental rates increase with increases in the temperature.

B. Physiological day degrees can be used to estimate the developmental period of an insect in the field given reliable temperature data from the habitat of the insect. The time of year and geographical location can dramatically affect the growth of an insect with respect to temperature.

IV. Effects of Climate on Populations

A. The combination of temperature, air movement, humidity, and rainfall can dramatically affect the success of a natural enemy in a given location. These variables considered together are equivalent to the term climate.

B. Examples of poor climate fit for introduced natural enemies:

1. Walnut Aphid (*Chromaphis juglandicola*) in California. In 1959 a solitary endoparasitic wasp, *Trioxys pallidus* was imported from Nice, France. By 1960 it was established from San Diego to Lompoc along the coast and interdiate valleys. Unfortunately it did not control the pest in the intermediate valleys. From 1960 to 1964 the parasite was introduced into Northern California, but was not recovered in most places. The French strain of parasite was able to undergo both estival diapause in the summer and hibernal diapause in the winter. It was originally collected in the coastal regions of France. It was decided that the parasite was climatically unfit for many of the walnut growing areas of California. Climatographic analysis of Nice, France suggests that the summer heat and possible dryness of Northern California and interior valleys of Southern California constituted the limiting factor in the spread of the parasite. A strain of *T. pallidus* imported from Teheran, Iran, by van den Bosch resulted in successful biological control in Northern California and the interior valleys. Climatographic analysis showed that Teheran was similar in climate patterns to Northern California walnut growing areas. The Persian strain had no summer diapause.

2. Alfalfa weevil, *Hypera postica* in California. This insect is distributed in 2 discontinuous areas in the state. One area in Northern California has "Great Basin Type" climate. In the southern areas there is a mild coastal pattern to typical continental, hot dry, cold-wet condition of California interior areas. Around San

Francisco there is a difference in the climate due to the interruption of the coastal marine influence by a series of relatively low, North-South mountain chains (Coastal Range). A parasite, *Bathyplectes curculionis*, was introduced in 1934 for control. It was a solitary endoparasitic ichneumonid. Prior to parasite's release, the alfalfa weevil was most abundant in the intermediate Coastal Range and least prevalent in the Central Valley. After the parasite's introduction, the weevil was least abundant in the Bay area and most abundant in the Central Valley. Good biological control was achieved. In the Bay area the parasite is active year round due to cool, humid summer conditions. In the Central Valley it is strongly suppressed by the summer heat.

V. Theories of Population Regulation and Change

A. Various theories have been suggested by noted insect population ecologists as to the way insect populations are regulated. The most warranted theories have been suggested by Nicholson, Andrewartha and Birch, Milne, Pimentel, and Huffaker.

B. **Nicholson: Divided controlling factors into**:

1. Density-legislative factors ("rule making") which was equivalent to density independent factors ("non-reactive" factors).
2. Density-governing factors ("rule enforcing") which was equivalent to density dependent factors. He believed that intraspecific competition was most important in regulating populations.

C. Andrewartha and Birch: They rejected the subdivision of the environment into physical and biotic factors because they did not believe it was a useful framework. They did work on 2 species in particular:

1. Swarm forming grasshopper, *Austroicetes cruciata*. Hypothesized that its distribution and abundance was determined by weather (Fig. 15.2).
2. Apple blossom thrips, *Thrips imaginis*. No density dependent factors could be found which controlled this species. See figure on page 1 of notes.

D. Milne: Took a "middle of the road" stance. He believed that abundance was a product of density independent and "imperfectly" density dependent factors. He considered intraspecific competition as the ultimately perfect density dependent factor.

E. Pimentel: Concept of "genetic feedback". Agreed with the concepts of density dependence and density independence and proposed that genetic feedback worked within the system. Genetic feedback: slight genetic change in host population which keeps it slightly ahead of the parasite until the natural enemy catches up by genetic change.

F. Huffaker: Divided environment into Conditioning Forces (Legislative factors) and Governing Mechanisms (Governing factors).

1. Conditioning forces: environmental factors or agents which, uninfluenced by density, contribute to setting of fixing of a framework of potential environmental capacity or affect interim population realization when capacity is not attained.
2. Governing Mechanisms: the actions of repressive environmental factors, collectively or singly, which intensify as the population density increases and relaxes as this density falls. Huffaker saw conditioning forces as setting up a frame in which the governing mechanisms worked.

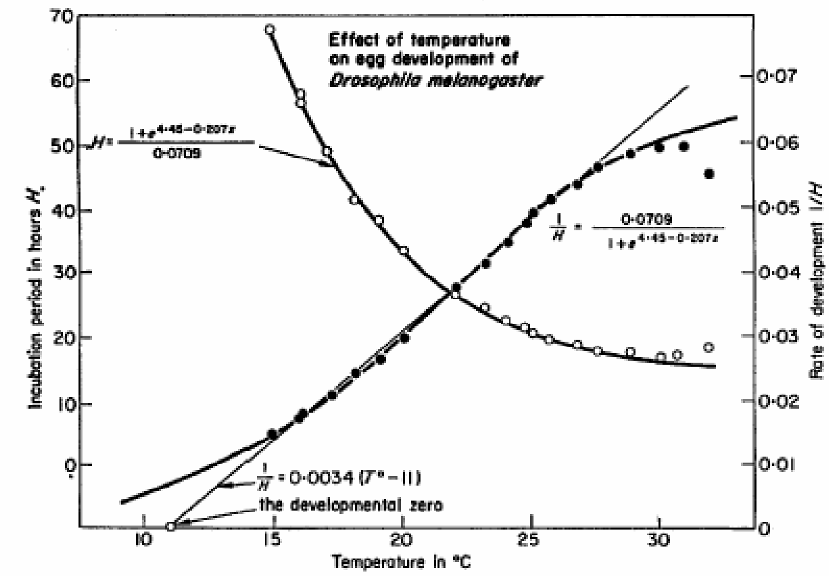

Fig. 15.1. Developmental times decrease with increases in the temperature and developmental rates increase with increases in the temperature. From Varley *et al.* (1974).

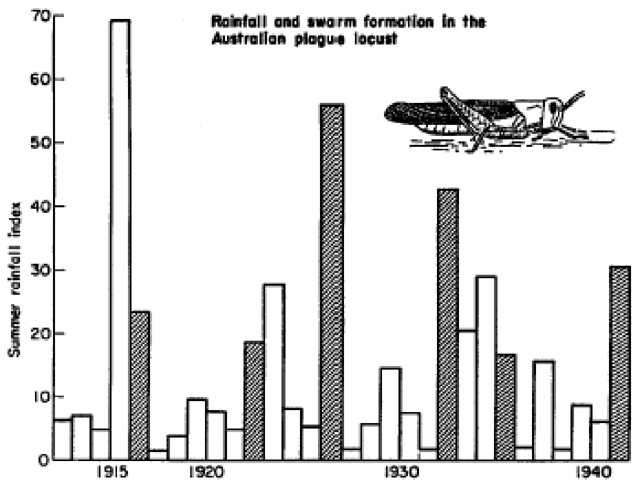

Fig. 15.2. Crosshatched bars represent the years in which the Australian plague locust, *Chortoicetes terminifera*, swarmed. The rainfall index was obtained by multiplying the total number of inches of rain from October to February by the number of those months in which there was more than 2 inches of rain (zero counting as 0.5 in.) Data were collected at Bogan-Macquarie, New South Wales, Australia. Figure from Varley *et al.* (1974); see for more information.