relatively moderate sea level rise (in a matter of 10–20 years), the frequency of extreme events (like cyclonic sea surges and coastal inundations), which are now very infrequent, may increase 10. The effects of such events on Third World countries can be cripling economically and in terms of human well-being. It will therefore be most crucial for every Third World country to have its own small team of scientists who can advise the government on the possibility of such occurrences and provide information on the level of reliability of the predictions, the options consistent with national relevance, and the precautionary steps to be taken.

Science and technology have become essential tools of development. Today's scientific research is tomorrow's technology. The scientific method and culture enable the people to develop the qualities of objectivity and rationality. It is therefore important for every Third World country to promote and support selected post-graduate teaching, training and research programmes that involve intellectual challenges and breed excellence

and generate manpower in science and technology. IGBP involves all the ingredients of a national priority effort—challenges in basic science at the cutting edge; new and unexplored challenges in interdisciplinary sciences; opportunities of international and regional cooperation; special relevance to Third World countries on whom the impact of global change will be most acute; and immediate application potential in diverse fields of national relevance.

- 1. Bull. Int. Soc. Soil Sci., No. 75, 1989, p. 25.
- 2. Dickinson, R. E. and Cicerone, R. J., Nature, 1986, 319, 109.
- 3. Ramanathan, V., Science, 1988, 240, 293.
- 4. Honghton, R. A. and Woodwell, G. M., Sci. Am., 1989, 260, 18.
- 5. Jouzel, J. et al., Nature, 1987, 329, 403.
- 6. Barnola, J. M., et al., Nature, 1987, 329, 408.
- 7. Grenthon, G., et al., Nature, 1987, 329, 414.
- 8. IGBP Report No. 4, 1988.
- 9. IGBP Report No. 6, 1988.
- 10. Private communication.

## Integrated entomology: Fact or fiction?

T. N. Ananthakrishnan

Very few biological ideas have lent themselves to such incisive and intensive discussion as the species concept, which has occupied and continues to occupy a central place in biological thought. The modern synthesis of Huxley<sup>1</sup>, involving the integration of Mendelian genetics into evolutionary theory, can be said to be a turning point, paving the way for a meaningful interpretation of the species. While classical biology has been essentially descriptive, the necessity to involve a functional component was considered obligatory to accommodate the emerging pluralistic views on selection levels, enabling a better appreciation of the several kinds of ecological interactions resulting in the recognition of population-dependent diversity. With increasing emphasis being laid on biological diversity, an understanding of the variations within and between individuals, populations, species and higher taxonomic groups, and of genetic diversity manifested in polymorphism and heterozygosity, has become obligatory. To be able to unravel possibly rare and unique genotypic and phenotypic traits, there is also a need for an assessment of how species respond to new environments—physical and chemical—and how evolution functions in species adapted to stresses. The numerical and species abundance of insects, which show large intraspecific diversity, and play a major role in

agriculture, medicine and forestry, naturally demands a multidimensional approach to entomological problems.

The recognition of the dynamic, plurimodal configuration of species has made it obligatory to adopt this integrated approach. However, in spite of the consciousness it has generated, it has not really taken off in this country, as is evident from the small number of publications. Everything revolves around the species—whether it be taxonomy, biosystematics, ecology, genetics, molecular biology or biotechnology. Species being dynamic, plastic elements changing their genetic constitution under the influence of the physical factors of the environment, the relationship between genotype and phenotype, and reproductive fitness become essential aspects. Population studies directed at establishing variation patterns appear essential and basic to the proper definition of taxa, so that there is a shift from form to process and pattern. Studies<sup>2-4</sup> on patterns of intraspecific diversity and implications of polymorphism in mycophagous Tubulifera have highlighted the degree of 'expression and suppression' of characters of individuals at different levels in a population, making taxonomic studies 'a communicable generalization of patterns discernible in natural diversity'. While alary polymorphism tends to result in ovarian diversity, a combination of this feature with oedymery and

gynaecoidy results in a variety of mating combinations and variations in egg output<sup>5</sup>. In the words of Dobzhansky (see ref. 6), the genotype does not give rise to the phenotype, but to a range of possible phenotypes. The 'norm reaction' is the entire range, the whole 'repertoire' of variant pathways of a given genotype in all environments—favourable, unfavourable, natural or artificial. Therefore the morphological species concept tends to mislead in cases of polymorphic diversity within species and has often far-reaching practical effects in the fields of biological control and medical entomology.

Though the degree of morphological differences is a useful criterion, a more meaningful approach is to integrate it with population studies in view of species being dynamic reproductive communities comprising ecological and genetic units involving a large, intercommunicating gene pool. The recognition of the role of pleiotropism affecting two or more characters is equally important, since the potential phenotypic effects of such genes have an important role in evolution. It suffices to indicate that both pleiotropism and polygenism tend to produce a multiplicity of phenotypes. Population-oriented ecological studies enable identification of polymorphism, so typical of insect populations, as well as a better appreciation of the diverse types of polymorphism—phenotypic, chromosomal, genic, balanced or transient, etc. Studies on chromosomal and genic polymorphism have widened the scope of ecological genetics, providing instances of genetic strategies in response to varying environments.

Many instances are on record where two or more allelic variants occur at the same gene locus and differential action of these alleles affects the chances of survival and reproduction. What is being emphasized is the direct relationship between the extent of genotype variation at a gene locus and the rate of increase in fitness of a population. Large-scale genetic variation has important implications. The best example would be insect resistance to pesticides, which has been recorded for about 250 species of insects. Genetic variants resistant to diverse types of pesticides tend to occur in every population subjected to pesticide treatment. The increasing problems confronted in biological control programmes, as well as the impact of biotypes or siblings in insect vector species, not to mention the frequent occurrence of intraspecific diversity in several pest species, have led to ecobehavioural, physiological, cytogenetical and biochemical approaches to a better assessment of the concerned species.

Biological data on food preference, habitat diversity, breeding sites and times, and behavioural diversity provide important insights. One has to keep in mind that the rate of increase of a population, as indicated by the innate growth-rate constant, resulting from internal physiological factors, also involves direct environmental

effects—interspecific and intraspecific competition and other kinds of interaction. Recognition of semeleparity or iteroparity among populations of a species or cyclical parthenogenesis or alternate mating strategies which also involve the impact of biochemical components of host tissues on the efficiency of reproduction, as well as bioenergetics involving the energy expended by different species or individuals of a species during their life cycle, has become meaningful components. Highly adapted differences between closely allied species still await discovery in relation to several species complexes through more intensive studies on the behavioural ecology of the species. Of immediate relevance to problems of applied entomology is the need to correlate taxonomic differences with adaptive differences. In this connection the occurrence of biotypes has added yet another dimension to population ecology. Several insects are known where reproductively isolated sympatric forms occur, which are morphologically indistinguishable. Interestingly the recombinants of their genes produce hybrid breakdown and developmental disharmony. There can be no better examples than several complexes known in the genus Drosophila. One of the most striking instances relate to the malarial vector Anopheles maculipennis in Europe, where six species were confused under this name, the adults being indistinguishable, but the diagnostic colour patterns of their eggs, the mode of arrangement of their egg-floats, mating habits and gene arrangements in their chromosomes confirmed this proven vector. Similarly Anopheles culicifacies chromosomes have been shown to be a complex with three siblings on the basis of chromosomal inversions and such forms have been known to have varying transmission rates<sup>7</sup>. Another striking instance relates to the differential ability of Nilaparvatha lugens the brown plant hopper to attack different rice strains. Differences in feeding behaviour, nutritional requirements, growth and reproduction, survival, isoenzyme patterns of insecticidal resistance are typical of the biotypes of many of these insect vectors of plant and human disease. The evolution of insect biotypes has also posed a fresh problem for forest pest management, since the differences in reproductive cycles between host and the insect tend to be considerably high with literally hundreds of insect generations during a single host generation time.

Another aspect demanding attention relates to the fact that in certain insects different degrees of mutual stimulation between individuals comprising populations of different densities lead to the appearance of distinct physical types or 'phases' which differ in their physiology and behaviour. Nowhere has this been proved better than in locusts which has enabled entomologists to recognize the solitary and gregarious phases and the role of play in locust biology. Such group effects are also known in several acridids, gryllids, as well as

lepidopteran caterpillars. Mention may also be made of several sibling species differing spectacularly in song patterns as in crickets and cicadas, the songs being associated with courtship and recognition behaviour.

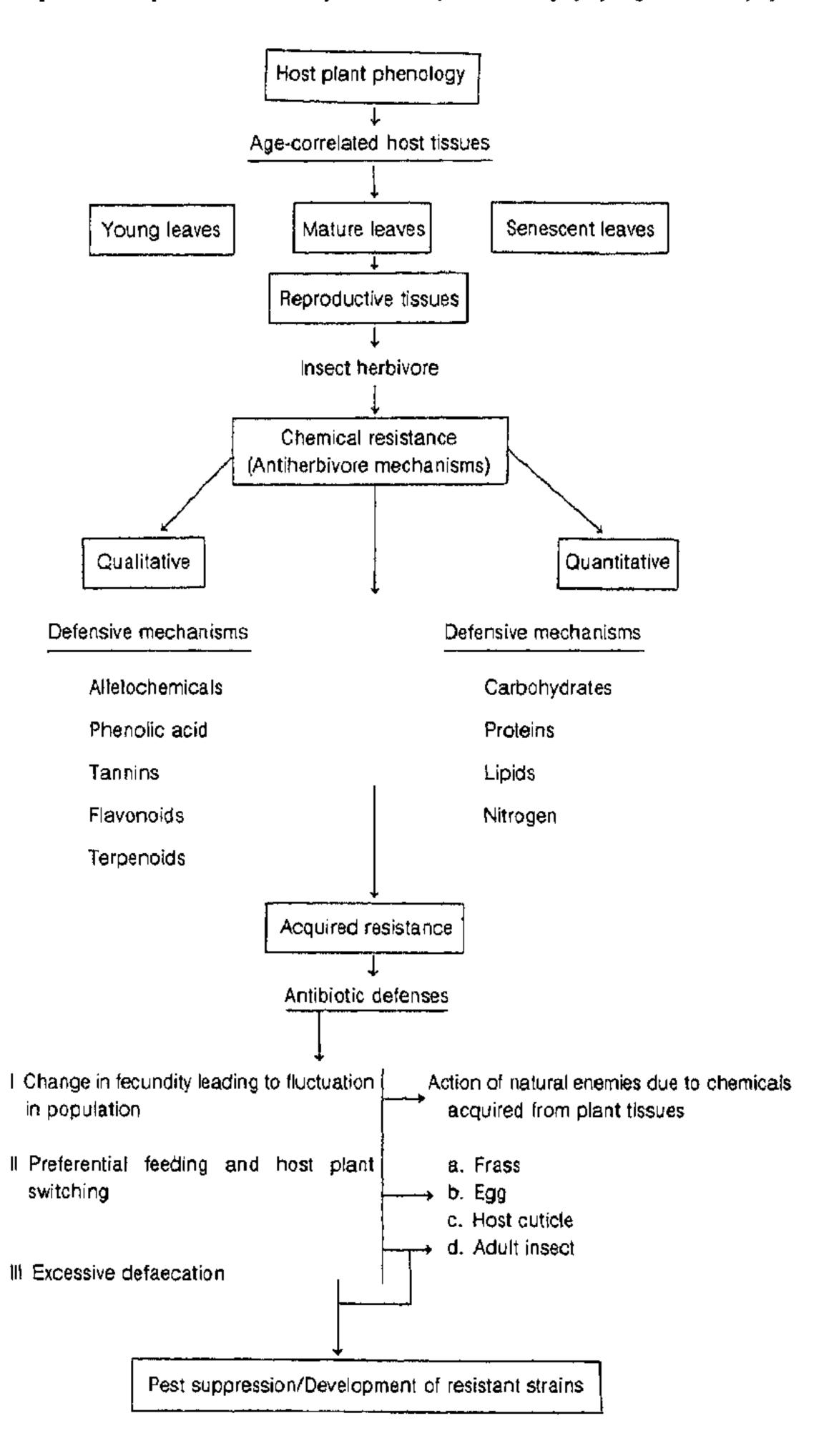
Photoperiod and form determination is an aspect that cannot be ignored in view of the production of diverse types of morphological inconsistencies within species. The structural diversity of male genitalia (so often used in determination of taxa), breaks down in several instances as in the case of the leaf hopper Euscelis lineolatus now known to be a complex of seven different seasonal forms, once described as distinct species<sup>8</sup>. Of equal relevance is the variation of ovipositor lengths relation to life cycle patterns and habitat preference. If closely related species prefer habitats of clearly different types, the habitat factors should differentiate ovipositor length; on the contrary if they share the same habitat, the life cycle differences would be a key factor in differential relation of ovipositor length<sup>9</sup>.

The utilization of modern techniques in biological research has further facilitated an indepth understanding of the dynamics of species. A better appreciation of cladogenesis or the process by which one species splits into two or more has been possible through genetic comparisons between species, genes with identical nucleotide sequences coding for identical proteins, and proteins with different amino acid sequences being coded by different genes. Biochemical and serological techniques with their ability to distinguish between macromolecules provide a most precise definition, implying a sort of comparative assessment at the molecular level. Diverse types of electrophoretic techniques from paper to polyacrylamide gel have adequately demonstrated their usefulness in protein studies. Since individual proteins characterize a particular species, a better appreciation of speciation results from a knowledge of protein structure. Combinations of procedures for studies on haemolymph proteins of insects make use of serology and electrophoresis. On the basis of limited studies on insect proteins it has been demonstrated that considerable variation exists, where their structure is modified over time. The 'protein' spectrum' concept has revealed that mutation and selection may alter or impart considerable structural variability to labile proteins, as in the case of haemoglobins and certain dehydrogenases etc., which have shown that they are capable of responding to selection pressures in the course of adaptation to the physical environment. One of the finest examples of biochemical characters as sensitive indicators of divergence relates to the blattids, where on the basis of GDH mobility (glucophosphate dehydrogenases) of their thoracic tissues through 'electrophoretic analyses, it has been possible to identify species-specific GDH fractions. In Trichogramma species isozyme analysis of different enzymes has enabled discovery of sibling species. The use of esterase isozyme analyses has been suggested for *Trichogramma* taxonomy which is complex and confusing. Electrophoretic banding patterns for malic enzyme, phosphoglucomutases and phosphoglucose isomers have enabled biochemical differentiation of 14 species of *Trichogramma*<sup>10</sup>.

Allozyme studies form a newly developed area focusing on adaptation at the population level. The biochemical phenotypes of many polymorphisms as indicated above are poorly understood, so that biochemical characterization of enzyme variants goes a long way in better interpretation of their adaptive significance. Such a study would interrelate allozyme function, physiological consequences and fitness differences. Intraspecific variation of the biochemical characters may even be sensitive indicators of divergence than morphological characters and such characters are useful in phylogenetic studies. Incidentally it may be indicated that phylogenetic systematics emphasizes that the multiplicity of structural differences between species can be more meaningfully interpreted through recognition of the fact that such differences between them as physiology, morphology, behaviour, ecology have evolved in the course of phylogeny<sup>11</sup>. Needless to say that with the availability of HPLC, GLC-MS-IR techniques it has become possible to determine the diversity spectrum of species-specific chemicals and incidentally the behavioural diversity of insects.

This leads us to the question of the role of host plants in the dynamics of insect species. Recent studies on the origin of insect races and speciation in certain phytophagous insects have led systematists to revise their ideas concerning speciation. Rapid establishment of new races by insects on introduced plants has led to suggest that races and species may arise sympatrically. This has been clearly demonstrated in the membracid Enchenopa binotata which is a polyphagous species. Biological differences existing among these insects native to each species of host plant have indicated genetic differences among host plant tissues. Studies on genetic differentiation between populations and host races indicate that the presence of alleles in high frequencies are fixed in one host race, absent or in low frequencies in another, suggesting that these host races represent separate gene pools<sup>12</sup>. Bush<sup>13</sup> suggested that shifts in host plant races promote sympatric diversity. Allochronic shifts in life histories or adoption of new host plants by phytophagous insects have been implicated in the formation of host plant races and reproductive isolation. An equally interesting example relates to the distribution of aphid species inducing galls on Pistacia. While they are generally host-specific, one species is known to occur on three host plants, but electrophoretic analyses revealed the consistent difference in esterase patterns, implying that although galls and

## Possible pathways of development of resistant pest strains/parasites in phytophagous insect population



the aphids are morphologically indistinguishable, they may be genetically different <sup>14</sup>.

Of added interest are the studies now pursued at the Entomology Research Institute relating to antibiotic effects of some secondary plant substances in regard to age-correlated biochemical changes of host plant tissues on insects, wherein larvae of the same species show behavioural diversity and changes in reproductive potential, besides the varied responses of biocontrol agents to the volatile and non-volatile substances of the frass of the insects, indicating the significance of such basic information on the behavioural dynamics of the species. The integrated entomology concept can nowhere be better illustrated than in the possible pathways of development of resistant pest strains/parasites in phytophagous insect populations (see chart).

Modern biochemical and genetic methodologies have enabled accumulation of very relevant data useful for biotechnology. Knowledge of the identity, distribution, bioenergetics of endemic organisms is a key resource for biotechnological research. The development of genetic libraries of diverse organisms and evolutionary questions of systematics are major driving forces for biotechnology/molecular biological areas. As such intimate inter-

actions between systematists, ecologists and geneticists in the identification of relevant species and traits for biotechnology application appear essential components<sup>15</sup>.

- 1. Huxley, J. S., Evolution-The Modern Synthesis, 1947.
- Ananthakrishnan, T. N., Ann. Soc. Entomol. Fr. (N. 5), 1968, 4, 413.
- 3. Ananthakrishnan, T. N., J. Bombay Nat. Hist. Soc., 1970, 67, 481.
- 4. Ananthakrishnan, T. N., Annu. Rev. Entomol., 1979, 24, 159.
- 5. Ananthakrishnan, T. N., Insect Sci. Appl., 1984, 8, 435.
- 6. Subba Rao, S. K. and Vasantha, K., Ann. Entomol. Soc. Am., 1983, 76, 985.
- 7. Subba Rao, S. K., Parasitology Today, 4, 72.
- 8. Beck, S. D., Insect Photoperiodism, Academic Press, 1980, p. 99.
- 9. Masaki, S., in *The Evolution of Insect Life Cycles*, Springer, Berlin, pp. 20-34.
- 10. Hennig, W., Annu. Rev. Entomol., 1965, 10, 97.
- 11. Hung, A. C. F. and Huo, S., Entomophaga, 1985, 30, 143.
- 12. Gutman, S. I., Wood, T. K. and Karhin, A. A., Evolution, 1981, 35, 205.
- 13. Bush, G. L., Annu. Rev. Ecol. Syst., 1975, 6, 339.
- 14. Koach, J. and Wool, D., Marcellia, 1977, 40, 207.
- 15. Kim, K. C. and Knutson, L., Foundation for a National Biological Survey, 1986, pp. 3-19.

T. N. Ananthakrishnan is Director, Entomology Research Institute, Loyola College, Madras 600 034.