

dedicated today, but before telling that story, the incredible story of the work on these sheets should be outlined.

'As you all know, Ramanujan returned to India in 1919 and died a year later. What is only now starting to be appreciated is the seriousness of his illness in England the previous two years. These pages are not dated, but from internal evidence they were written late in Ramanujan's life, much of it in his last year. Two thirds of the pages deal with basic hypergeometric series and most of this work is significantly deeper than Ramanujan's earlier work on the same subject. Try to imagine the quality of Ramanujan's mind, one which drove him to work unceasingly while deathly ill, and one great enough to grow deeper while his body became weaker. I stand in awe of his accomplishments; understanding is beyond me. We would admire any mathematician whose life's work was half of what Ramanujan found in the last year of his life while he was dying.

'Some of Ramanujan's work has one quality which is shared by very little other work. Most mathematics, including some very good work, is predictable. Much of the rest seems inevitable after it is understood, and it would eventually be discovered by someone else. Little of Ramanujan's work seems predictable at first glance, and after we understand it there is still a fairly large body of work about which it would be safe to predict that it would not be rediscovered by anyone who has lived in this century. Then there are some of the formulas Ramanujan found that no one understands or can prove. We will probably never understand how Ramanujan found them.

'The story of the thread from these sheets to the bust is simple. Andrews has done a lot of very deep work trying to understand what Ramanujan discovered. Eventually *The New York Times* heard about it and interviewed him. *The Hindu* followed with a more extensive interview, and also published an interview with Ramanujan's widow, Janaki Ammal. She lamented the fact that a statue of Ramanujan had never been

made, although one had been promised. Andrews sent me copies of these interviews, and after a couple of months my subconscious finally got through to my conscious mind and it was clear that a bust should be made. Since Janaki Ammal was 80, time was important, so it was up to individuals rather than governments or societies, since institutions move slowly. My first reason for wanting a bust was simple; if Ramanujan's widow wanted one she should have it. That was the least we could do to show our appreciation of Ramanujan to someone who had been a great help to him. Later I realized there was a second reason, which Janaki Ammal must have realized all along. She knew Ramanujan, and while she did not understand his mathematics, she knew that he was one of the few whose work will last. As long as people do mathematics, some of Ramanujan's work will be appreciated. Fame is a strange thing and is often fleeting. An interview on a television programme is now the accepted form of honor. In Ramanujan's case a more permanent memorial is appropriate: one which can be appreciated by those who do not understand his mathematics should be added to the memorial Ramanujan made for himself with his work.

'I am pleased to have played a role in this, and would like to thank the more than one hundred mathematicians and scientists who contributed money for the bust which was presented to Janaki Ammal. The bust being dedicated today was donated by a couple who are now friends, Subrahmanyan and Lalitha Chandrasekhar. When I asked Chandra about the appropriateness of a bust of Ramanujan, he immediately replied that it was a good idea and they would do all they could to help. They did. Finally I want to thank the sculptor, Paul Granlund. While he does not appreciate Ramanujan's mathematics as those of us who have studied it do, he studied Ramanujan's passport photo deeply, and the results show in the bust. He probably understands some things about Ramanujan that we do not.'

Chemical ecology in biological control

T. N. Ananthakrishnan

Biological control of insect pests of plants is now recognized as part of the allelochemical web entangling plant and insect communities. For increased efficiency in biological-control programmes, an intimate knowledge of chemical ecology is obligatory. This article examines the implications of chemical ecology in biological control.

Chemical ecology is concerned with communication of signals through specific chemicals between organisms in an ecosystem^{1,2}. It has become dominant in understanding insect-plant interactions. Signalling chemicals that an organism can detect in its environment and which may affect the organism's behaviour or physiology are called semiochemicals. Those that act between members of the same species are called pheromones, and those that act between species are called allelochemicals. The latter may be allomones, which favour the emitter, or kairomones, which favour the receiver. Many allelochemicals act as both allomone and kairomone; such chemicals are called synomones. While the insect sex pheromones are the best-known semiochemicals, plants are known to produce a wide variety of allelochemicals that influence plant-insect relationships. These include repellants, feeding or oviposition deterrents, and antibiosis factors (allomones); and attractants, oviposition excitants, and feeding stimulants (kairomones).

Plant and insect coevolution

The emergence of chemotypes in plants as well as of races or biotypes in insects is a response to selection pressure exerted by insects and plants on each other: plants develop new chemicals against insects and insects develop detoxification systems, enabling each to enter a new 'adaptive zone' and resulting in diversity³. In other words, there is the possibility that adaptive radiation of plant chemicals followed by plant speciation occurred as a result of intense herbivore pressure⁴. This diversity in turn created selection pressures leading to behavioural and biochemical adaptation in phytophagous insects, and the development of 'specialists' and 'generalists', so classified in accordance with their ability to survive on a range of host plants and detoxify plant toxins. The more an insect specializes on a group of related plants, the more the plants tend to diversify through the development of new toxins produced as secondary metabolites. There can be no better examples than the plant groups expressing the coumaric acid-hydroxycoumarin-furanocoumarin system⁵ as a response

to habitual feeding by specialized insects. Some oligophagous species have become adapted to furanocoumarins by behavioural and physiological means, indicating that plant secondary metabolite chemistry greatly augments the organic diversity of both insects and plants. Different insects tend to respond differently to furanocoumarins, and changes in chemical phenotype will affect different species differently⁶. Insect biotypes have now come to be increasingly recognized, with each biotype clearly growing best on its own host plant, the differences between biotypes being due to differences in behavioural responses to 'repellent' or 'stimulant' chemicals⁷.

Allelochemical web

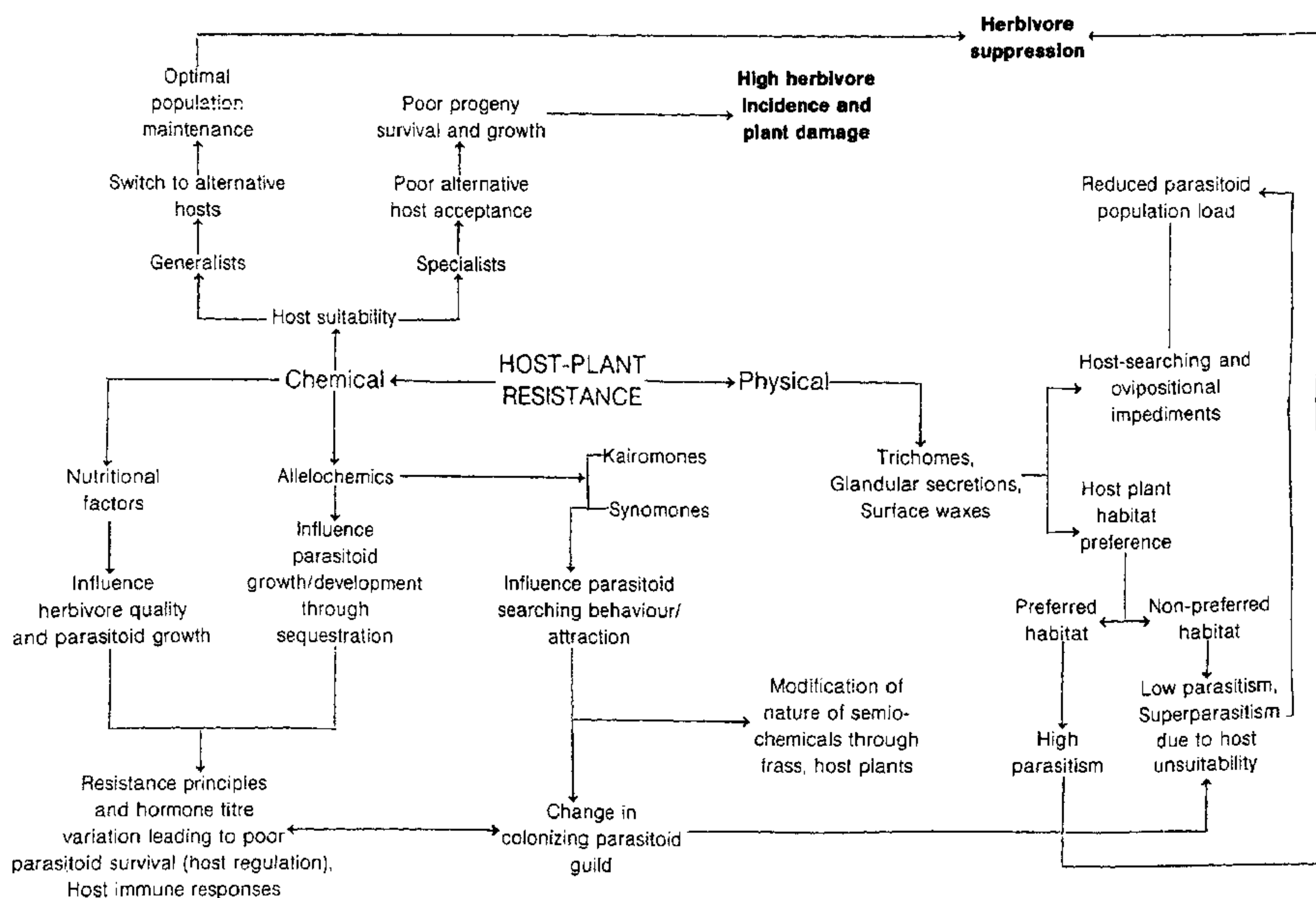
Insects, including those that are plant pests, have natural enemies, which are often other insects. These enemies may be parasites, predators or parasitoids. A 'parasite' is usually much smaller than its 'host', and a single individual usually does not kill the host. A 'predator' is a free-living organism that is usually larger than its 'prey', kills the prey, and requires more than one prey during its development. A 'parasitoid' is a special kind of predator, is often the same size as its host, kills the host, and requires only one host (prey) for development into a free-living adult. One can distinguish between naturally occurring biological control, and applied biological control, which involves the use and manipulation of natural enemies of pests by man, although the term biological control has itself traditionally been used for the latter. Biological control is intimately linked with the allelochemical web of plant-pest-parasitoid/predator, resulting in a tritrophic or sometimes a tetratrophic level of interaction. For effective manipulation of the communication systems involved in this complex allelochemical relationship, an understanding of the direct or indirect, beneficial or detrimental effects of plant secretions on phytophagous insects and their natural enemies is important. While phytophagous insects are capable of specializing on toxic plants and obtain protection against natural enemies through sequestration of such substances as cardiac and cyanogenic glycosides and alkaloids,

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

parasitoids and predators have also developed the ability to sequester these toxic chemicals from the host insects. The behaviour of parasitoids towards each of the biotypes of a host species is an aspect deserving consideration. Generalist and specialist predators and parasites also tend to provide a major driving force in the evolution of a specialized host (plant) range for phytophagous insects, and restriction in host (insect) range of many parasitoids might be important in causing host switches or broadening of host (plant) range of phytophagous insects⁸. Besides the influence of host physiology on the fitness of parasitoids and the effects of plant physiology and plant allelochemicals on the biology of parasitoids and predators⁹, there is a need to assess allelochemical effects on parasitoid success and fitness, since some of these may prevent normal nutrient utilization or cause inhibition of enzyme systems¹⁰. Quantitative and qualitative differences in the nutritional and allelochemical composition of the host insects tend to have a significant impact on the parasitoids¹¹, and, in parasitoid–host relationships, the future development of the host is important to the parasitoid.

Phytochemicals can not only act as attractants for

pests, but, in some cases, also elicit from parasitoids of these pests an intense searching behaviour, by which the parasitoids seek their host insects which have accumulated these chemicals. Thus natural enemies of phytophagous insects may use the same chemicals to locate the host plant and the insect. (Such chemicals are examples of synomones, since the phytophagous insects benefit as receivers and the host plants benefit as emitters by attracting natural enemies of the former.) Parasitoids are often attracted to plants on which their hosts feed, and damaged plants may provide stimuli for increased parasitoid searching. In the absence of a significant role of plant-derived compounds in insect defence, shifts to chemically unrelated plants could be expected. While plant odours or floral scents attract or arrest natural enemies, some relatively odourless crucifers, in response to attacking insects, produce enzymes that quickly convert inactive mustard oils to volatile parasitoid-attracting derivatives¹². In such a situation also, a shift to a different plant may enable a phytophagous insect to escape from parasitoids that use plant compounds as host-finding cues¹³. Parasitoids and predators thus tend to favour adaptive radiation of phytophagous insects into new, 'enemy-free space' that



Interplay of host-plant physical and chemical factors in host plant-phytophagous insect (herbivore)-parasitoid assemblage—an allelochemical web.

other plants may provide¹⁴. On the other hand, plant allelochemicals may also have the effect of prolonging the developmental stages of an insect, leading to increased exposure to parasites and predators.

Programming or imprinting to specific plant environments is typical of some parasitoids. Some plant chemicals from the host that are important in host location are short-range host cues that orient the parasite only within a short distance. They are not very volatile, requiring high concentrations to elicit a response. Some are 'contact' cues and are perceived and elicit response only on physical contact of parasitoid with host. Compounds eliciting ovipositor probing upon contact¹⁵ are known. Such contact chemicals are present in host frass. Semiochemicals mediating host-finding emanate from frass; mandibular, labial and other secretions; exuviae; moth scales; and damaged plant tissues associated with the host. The long-chain hydrocarbon tricosane in moth scales has been reported as a kairomone for species of *Trichogramma*, a parasitoid wasp; this substance elicits and maintains host-seeking behaviour. Volatile chemicals from the oviposition gland of *Heliothis* are also known to be involved in host-searching behaviour of *Trichogramma*. The quality of the host egg that *Trichogramma* has access to may also be important: altering the diet of *Corcyra cephalonica*, another host of *Trichogramma*, results in eggs of varying quality, and the fecundity of *Trichogramma* varies with differences in host eggs (unpublished). It is well known that another parasitoid wasp, *Microplitis*, which is a larval parasitoid, responds more strongly to the frass of *Heliothis zea* fed on cowpea and to soybean-reared *Heliothis* larvae than to frass of larvae or larvae fed on corn^{16,17}. Related strains or chemotypes of a given plant also tend to differ in attraction if their volatile-chemical profiles are different. However, females of successful parasitoids are capable of responding to more than one or a combination of cues. The influence of plant as well as insect allelochemicals on natural enemies of pests provides a good instance of the role of chemical ecology in biological control.

Analysis of plants has shown that chemical substances such as resorcinol, phloroglucinol, gallic acid, pyrogallol and tannic acid have tissue-specific distribution within the plant. The effects of these compounds on phytophagous insects such as *Heliothis armigera* and *Spodoptera litura* include reduction in their food utilization efficiency, excessive defaecation, and prolonged larval duration exposing the larvae to more parasitoids and predators¹⁸. The effects of the resistance principles of a given plant are not common to all species of phytophagous insects utilizing it as host plant, but there is differential susceptibility of even closely related species¹⁹. One of the current projects at the Entomology Research Institute concerns the diversity of allelo-

chemicals in different cultivars of cotton as well as the nature of the volatile chemicals in frass of cotton pests, and the effects of these chemicals on parasitoids.

New plant varieties may influence natural enemies of pests directly via altered levels of attractants and repellents, such as trichome toxins²⁰, or indirectly through physiological effects on the phytophagous hosts. There is a suggestion that plant breeders should strive to evolve varieties with reduced levels of substances attractive to phytophagous insects but increased levels of substances attractive to natural enemies. The same substances may play both roles, as in the case of allylisothiocyanate, which is stimulating to both the cabbage aphid and its parasitoid²¹ (an example of a synomone). Breeding for increased flowers, nectar, extrafloral nectaries and blooming period tend to increase survival of natural enemies. Plant allelochemicals have a complex effect on plant fitness in a given environment: they modify the behaviour of associated phytophagous insects, in turn affecting the quality of the latter as a resource for associated parasitoids²². The relative fitness of individuals varies with the environment and host-parasitoid/predator competition is part of the environment, biotic and abiotic²³. Particular chemical fitness traits in an individual may be adaptive only under a particular set of environmental conditions.

Role of micro-organisms

While studying plant natural products as a component of a tritrophic system provides an understanding of the consequences of their sequestration by host insects on parasitoids, the impact of pesticides and bacterial insecticides on non-target organisms, including beneficial organisms, must be examined more critically. Micro-organisms play a wide variety of important roles in plant-insect relations. Some microbes chemically mediate interactions between phytophagous insects and their parasitoids and predators. Micro-organisms associated with insects are known that produce pheromones. The natural enemies of phytophagous insects may also sense semiochemicals that emanate from these micro-organisms²⁴. There are also instances where toxic substances or viruses are injected into host insects during oviposition by parasitoids. Of great interest is the finding that the 'calyx fluid' surrounding the eggs of some parasitoids, which has been shown to contain a type of virus, suppresses host immune reactions. Recent findings show that, besides calyx fluid, the contents of the poison glands also influence immune reactions²⁵. One of the most dynamic aspects of parasitoid biology is the role of viruses in parasitoid-host relationships. The role of micro-organisms in the ecology of insect-plant relations is emerging as an important aspect of the tritrophic interaction.

Integrated pest management

Recent approaches to biological control have involved altering the endocrine balance of pests. The physiology of these insects, including their hormonal status in different stages of development, plays an important role in determining their suitability as hosts for parasitoids. While it is known that the parasitoids themselves modify host physiology to their own benefit, host regulation also occurs, and may be structural, behavioural, nutritional, physiological, biochemical or developmental²⁶. Parasitoids are faced with problems of nutritional specificity of hosts, their size, age and nutritional history affecting parasitoid development. A combination of nutritional and hormonal factors determines host suitability²⁷.

Genetic engineering has the potential to provide crop plants with novel and potent resistance factors. Genetic engineering techniques will enable 'slipping in' of a new resistance factor whenever a particular resistance factor tends to become 'obsolete' owing to pest evolution²⁸. Plant toxins generally tend to reduce the quality of pest insects as hosts for parasitoids. Interestingly, however, Vinson and Williams report (unpublished) that gossypol in cotton, while inhibiting development of *Heliothis*, a pest, promotes development of parasitoids of the pest. The possibility that insect neurohormone genes could be inserted into the genomes of plants, resulting in the transformed plants producing the hormone and disrupting the physiological balance of phytophagous insects²⁹, may also pose a threat to the survival of parasitoids. This calls for engineering plant defence compounds that reduce insect pest damage and at the same time are compatible with use of beneficial insects.

Needless to emphasize, quality control of eggs of beneficial insects, their nutritional and genetic improvement, and behavioural manipulation of mass-released beneficial insects are important aspects of efficient biological control of pests. While the use of host-plant resistance involves increasing levels of allelochemicals that confer antibiotic effects, there is the need to consider the fact that parasitoids and predators tend to be more sensitive to toxic substances than their hosts. Mass-produced parasites may be ill-prepared to deal

with the 'biochemical milieu'³⁰ that they have to face within the host in the field and with the fact that this milieu will vary from host to host.

1. Greenblatt, J. A. and Lewis, W. J., *Environ. Management*, 1983, 7, 35.
2. Ananthakrishnan, T. N., *Proc. Indian Acad. Sci. (Anim. Sci.)*, 1990, 99, 177.
3. Ananthakrishnan, T. N., *Dynamics of Insect-Plant Interactions* Oxford and IBH, New Delhi, 1986.
4. Spencer, K. (ed.), *Chemical Mediation of Coevolution* Academic Press, New York, 1988, pp. 128-129.
5. Berenbaum, M., *Ecol. Entomol.*, 1981, 6, 345.
6. Berenbaum, M. R. and Zangerl, A. R., in *Chemical Mediation of Coevolution* (ed. Spencer, K.), Academic Press, New York, 1988, p. 128.
7. Futuyama, D. J. and Leterneau, M. S., *Coevolution*, Sinauer Associates, 1983, pp. 207-231.
8. Bernays, E. M. and Graham, *Ecology*, 1988, 69, 886.
9. Boethel, D. U. and Eikenberry, R. D., *Interactions of Host Plant Resistance and Parasitoids and Predators of Insects*, 1986.
10. Barbosa, P. and Letourneau, P. K., in *Novel Aspects of Insect-Plant Interactions* (ed. Barbosa, P.), John Wiley, New York, 1988.
11. Vinson, S. B., *Archiv. Inst. Biochem. Physiol.*, 1990, 13, 63.
12. Shmida, H. and Auzebach, M., *Isr. Land Natur.*, 1983, 9, 61.
13. Vinson, S. B., *ISI Atlas Anim. Plant Sci.*, 1988, 1, 25.
14. Gilbert, L. E. and Sanger, M. C., *Annu. Rev. Ecol. Syst.*, 1975, 6, 365.
15. Vinson, B., in *Evolutionary Strategies of Parasitic Insects and Mites* (ed. Price, P. W.), Plenum, New York, 1988, pp. 14-48.
16. Nordlund, D. A. and Lewis, W. J., *Entomol. Exp. Appl.*, 1985, 38, 109.
17. Nordlund, C. E. and Sauls, D. A., *Chem. Ecol.*, 1981, 7, 1057.
18. Ananthakrishnan, T. N., *Proc. Indian Acad. Sci. (Anim. Sci.)*, 1990, 99, 39.
19. Ananthakrishnan, T. N., Annadurai, R. S., Senrayan, R. and Murugesan, S., *Phytophaga*, 1990, 3, 55.
20. Jones, D., *Entomophaga*, 1986, 31.
21. Read, D. P. and Feeny, P. P., *Can. Entomol.*, 1970, 1567.
22. Vinson, S. B., in *Insect Communication* (ed. Lewis, T.), Academic Press, London, 1984, pp. 325-348.
23. Berry, R. J., *Oikos*, 1985, 44, 222.
24. Dicke, M., in *Novel Aspects of Insect-Plant Interactions* (ed. Barbosa, P.), John Wiley, New York, 1988, pp. 125-163.
25. Vinson, B., *Annu. Rev. Entomol.*, 1976, 21, 109.
26. Vinson, S. B. and Iwantsch, G. G., *Quart. Rev. Biol.*, 1980, 55, 143.
27. Bloem and Duffey, *Entomol. Exp. Appl.*, 1990, 54, 141.
28. Gould, F., *Bioscience*, 1988, 38, 26.
29. Schneiderman, H. A., *Bull. Entomol. Soc. Am.*, 1984, 30, 55.
30. Barbosa, P., *Proc. 5th Int. Symp. Insect-Plant Relationship*, Wageningen, 1982, pp. 63-70.