

16. Nita Dilawar, S., Sah, B. R., Mehta, V. D., Vankar, D. K., Avasthi, and Mehta, G. K., *Vacuum* 1996, **47**, 1269.
17. Dhuri, P., Ajay Gupta, S. M., Chaudhuri, D. M., Phase, and Avasthi, D. K., *Nucl. Instrum. Methods B*, 1999, **156**, 148.
18. Gupta, R., Ajay Gupta, D. K., Avasthi, G., Principee, and Tosello, C., *Nucl. Instrum. Methods B*, 1999, **156**, 153.
19. Paul, A., Ajay Gupta, Choudhari, S. M., Phase, D. M. and Avasthi, D. K., *Nucl. Instrum. Methods B*, 1999, **156**, 158.
20. Ajay Gupta, A., Paul, Ratnesh Gupta, Principee, G. and Avasthi, D. K., *J. Phys. B, Condens Matter Phys.* 1998, **10**, 9669.
21. Townsend, P. D., *Nucl. Instrum. Methods B*, 1990, **46**, 18.
22. Aithal, S., Nagaraja, H. S., Mohan Rao, P., Avasthi, D. K. and Sarma, A., *J. Appl. Phys.*, 1997, **81**, 7526.
23. Chakravarti, S. K. and Vetter, J., *Nucl. Instrum. Methods B*, 1991, **62**, 109.
24. Vetter, J. and Dobrev, D., *Nucl. Instrum. Methods B*, 1999, **156**, 177.
25. Biswas, A., Avasthi, D. K., Singh, B. K., Lotha, S., Singh, J. P., Fink, D., Yadav, B. K., Bhattacharya, B. and Bose, S. K., *Nucl. Instrum. Methods B*, 1999, **151**, 84.
26. Reber, N., Omichi, H., Spohr, R., Tamada, M., Wolf, A. and Yoshida, M., *Nucl. Instrum. Methods*, 1995, **105**, 275.
27. Vetter, J., GSI Darmstadt, Germany (private commun.).
28. Mittal, V. K., Lotha, S. and Avasthi, D. K., *Radiat. Eff. Defects Solids*, 1999, **147**, 199.
29. Trautmann, C., *Nucl. Instrum. Methods B*, 1995, **105**, 81.
30. Avasthi, D. K., Singh, J. P., Biswas, A. and Bose, S. K., *Nucl. Instrum. Methods B*, 1998, **146**, 504.

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## Phenotypic flexibility of plants and adaptive dynamics of specialist–generalist insects

T. N. Ananthakrishnan

*Host plant flexibility resulting in intraspecific variation enables plants to assume the most adaptive phenotypes in a particular environment, significantly altering the performance and fitness of phytophagous insects. The structural diversity of plants over time has created a selection process leading to behavioural and biochemical adaptations resulting in specialist and generalist insects. With host plant populations comprising phenotypically heterogenous individuals, insects have the potential to adapt to an individual plant's chemical profile. The potential role played by plant signals in modulating and inducing the biosynthesis of many secondary metabolites has become an important aspect of insect–plant interactions which have relevance in agriculture.*

INTENSIVE studies on diverse aspects of insect–plant interactions have emphasized the role of a bewildering number of secondary plant chemicals in enabling both wild and cultivated plants to cope up with insect attack. The evolution of insect–plant associations has been invariably guided by the plant chemistry which set the stage for the extensive radiation of herbivorous insects<sup>1</sup>. The ability of insects to identify preferred hosts is astounding, each species being endowed with unique sensory systems enabling recognition of its host plant range based on relevant cues, as well as adjusting to continually changing plant conditions. While entomocentrism involving host preferences tends to vary among individuals or populations causing them to select different diets, phytocentrism emphasizes

the role of genetic variation in plants which influences the association of insect species on phenotypically flexible plants<sup>2</sup>. Nevertheless it cannot be denied that plants have a significant effect on insect evolutionary changes or strategies from a chemical viewpoint and play a fundamental role in insect population dynamics<sup>3</sup>. The chemical diversity of host plants has posed the problem of fitness and adaptation in insects calling for an equally efficient physiological adaptation in plants to overcome the barriers of feeding and oviposition.

While host choice for mating and oviposition has ecological and evolutionary implications, relevant insect adaptations are shaped by contemporary ecological forces<sup>4</sup>. The optimal defence and resource availability hypotheses explain the qualitative and quantitative patterns of plant defences<sup>5–8</sup>. The optimal defence hypothesis assumes that herbivory is the primary selective force shaping quantitative patterns of secondary metabolism, the resource availa-

T. N. Ananthakrishnan lives in Flat 6, 'DWARAKA', 22 Kamdar-nagar, Chennai 600 034, India.

bility hypothesis<sup>9,10</sup> supplements it by predicting that the optimal level of defence will vary with the growth rate of the plant. The adaptive value of host chemicals becomes important to the extent that the biosynthetic variability of plants coupled with their multifaceted roles have enabled them to become the primary agents in the ecological and evolutionary dynamics of insect-plant interactions. Information presented here essentially deals with some aspects of phenotypic plasticity of plants and their adaptive diversity of specialist and generalist herbivorous insects. The significance of constitutive and induced resistance in plants as well as aspects regarding the adaptive dynamics of insects to a plant's unique chemical profile have been discussed here.

### Phenotypic plasticity

Plants are known to adequately respond to environmental changes and phenotypic plasticity is an adaptation to such fluctuations resulting in varied expression of such traits<sup>11</sup> as that of the chemical characters of a plant. The adaptive value of host plant chemicals becomes relevant to the extent that their biosynthetic variability coupled with their multifaceted roles have enabled them to become primary agents in the ecological and evolutionary dynamics of insect-plant interactions<sup>12</sup>. The potential adaptiveness of phenotypic plasticity is well recognized, enabling plants to assume the most adaptive phenotype in a particular environment 'buffering the effects of spatial and temporal variation in resource availability'<sup>13</sup>. The chemical phenotype of a plant may differ considerably from other individuals in a population due to the genetic and environmental variation in chemical traits. Although host suitability can be a function of structural, physiological or habitat characters associated with the plants, allelochemicals are the major determinants of host suitability. Intraspecific variation in host plant resistance has become an important area of research, since subtle variations in the quality and quantity of specific allelochemicals can significantly alter the preference and performance of phytophagous insects on a given host. The host plant populations must comprise phenotypically heterogeneous individuals so that insects have the potential to adapt to an individual plant's chemical profile. As such the role of intraspecific differences in plant chemistry in the differential utilization of host plants have now been recognized resulting in variability in insect distribution<sup>14</sup>.

### Chemical diversification in host plant and insect interactions

One of the features of secondary metabolism to cope with and adapt to a continually changing environment relates to chemical diversification, with intra population variation being inherent in secondary metabolism. Increased chemi-

cal diversity and intra population variation of secondary metabolism are evolved under the selection pressure of the environment<sup>12</sup>. The potential of phytophagous insects to exert selection in patterns of secondary metabolites within plants is reflected by the phylogenetic patterns in angiosperms, indicating that the trend has been towards the evolution of more toxic secondary metabolites<sup>15,16</sup>. The diversity of biogenetic pathways in plants is therefore of significance in that some of them lead to one or a few metabolites from which numerous derivatives are formed by enzymatic transformation such as phenylpropanoids, alkaloids and mono-di- and sesquiterpenes. Intraspecific variation in secondary metabolism is equally evident with these chemical substances specifically intergrated with the developmental programme of plants.

Insect damage also results in induced defences which are chemically heterogeneous, different mechanisms operating in different regions of the plant, a single damage simultaneously inducing levels of multiple defence chemicals. Induction may be an important component in the generation of phenotypic plasticity in plant chemistry. Induction may increase variation in defence chemistry both within and between plants so that 'an induced plant is a mosaic of defence chemistry'<sup>17</sup>. Many species of Brassicaceae exhibit accumulation of glucosinolates after damage by insects with individual plants varying in the level of glucosinolates over time. Similarly feeding by papilionids on umbelliferous plants also results in changes of furanocoumarins<sup>18</sup>. The distance from the site of injury, amount of damage and type of elicitors involved determine the speed of biosynthesis. In view of the ability of insects to overcome plant toxins, a plant should produce several allelochemicals or their groups which involve several biosynthetic pathways. For instance, plant isomeric compounds such as xanthotoxin and bergapten in wild parsnip (*Pastinaca sativa*) tend to have a profound effect on growth, survivorship and fitness of insects such as the parsnip webworm *Depressaria pastinacella*<sup>19</sup>. Besides, synergistic interactions between allelochemicals contribute an important element in a plant's chemical protection and some of the notable examples are xanthotoxin and myristicin<sup>20</sup>, fusaric acid and gossypol<sup>21</sup>, *cis* asarone and menthol<sup>22</sup>, to mention a few.

Plant community structure can influence insect herbivore population growth and host plant quality in a variety of ways. Heterogeneity in structure and chemical components of plants interferes with the exploitation of host plants by insects and notable instances of the varying degrees of resistance are shown by the increasing numbers of cultivars in several crops. For instance, cotton cultivars show varying degrees of resistance to *Helicoverpa armigera* through varying concentrations of gallic and salicylic acids, phloroglucinol, resorcinol and gossypol<sup>23</sup>. Increase of insect abundance depends on the combination of such dimensions as host plant species, host plant organs as also plant abundance, size and architecture and efficiency of

defence mechanisms, while plant chemistry 'decisively determines the composition of herbivore insect assemblages'<sup>24</sup>. Variation in resistance besides influencing the ability to survive and reproduce on a particular genotype also tends to influence the evolution of many insect characters.

### Adaptive diversity in specialist and generalist insects

Plants are able to synthesize a variety of chemical substances such as non-protein amino acids, alkaloids, terpenes, flavonoids and their chemical diversity has increased greatly during the course of evolution along with periodical changes in insect feeding pressure. This diversity in turn created a selection process leading to behavioural and biochemical adaptation in insects resulting in specialists and generalists. Contrasting selection pressure exerted by them possibly explains the degree of variation in concentration of allelochemicals in natural plant populations, very high concentrations deterring the generalists, but not the specialists. Further, specialists lack adequate variation to adapt to a greater range of host species, while generalists are invariably polyphagous, a new host plant being an extension of its diet breadth, the direction of host shifts being genetically constrained. Among several instances of host shifts, an interesting case is that of *Retithrips syriacus* (Thysanoptera), a polyphagous species heavily infesting castor (*Ricinus communis*, Euphorbiaceae), and which has successfully adapted to hosts like *Eucalyptus globulus* (Myrtaceae) and *Manihot utilitissima* (Euphorbiaceae), over a period of time, overcoming the terpenoid and cyanogenic compounds, respectively<sup>25,26</sup>. Papilionid butterflies offer excellent instances of specialist and generalist species.

The genus *Papilio* has been utilized for studies relating to different degrees of genetic separation between populations<sup>27</sup>. Several species of butterflies use different hosts in different regions and separate populations are likely to be subjected to differential selection pressures. Many examples of intraspecific population dynamics are known. Some *Papilio* species use Rutaceae plants as specialists but populations use different food plants in various parts of their range<sup>28</sup>. *Battacus philenor*, a specialist species of *Aristolochia* (encountering aristolochic acid) and *Papilio polyxenes*, also a specialist on species of Apiaceae and Rutaceae (encountering furanocoumaric acid) and the generalist *Papilio glaucus* feeding on plants of more than 20 natural orders (encountering phenolic and cyanogenic glycosides), adopt different approaches to detoxification or sequestration of host plant compounds<sup>29</sup>.

While plant families are characterized by a particular group of allelochemicals such as glucosinolates (Cruciferae), cardenolides (Asclepiadaceae), iridoid glycosides (Scrophulariaceae), etc. variations among population of

single species and among individuals of a population and parts of a single plant may vary so that qualitative and quantitative variation in allelochemical profiles of plants tends to be an important determinant of patterns of herbivory. An interesting instance of growth inhibition in *Helicoverpa zea* larvae in corn has been shown to be due to different silk maysins<sup>30</sup>, a C-glycosyl flavone and related compounds like chlorogenic acid and apimaysin. Iridoid glycosides may exert considerable diversity in feeding preferences, the generalist surviving less well on diets with the iridoids, while the specialist performed best on diets with two iridoid glycosides such as catalpol and acubin in *Plantago lanceolata*<sup>31</sup>. The relative amounts of different iridoid glycosides may vary substantially from one population to another. Patterns of variation in host chemistry and insect responses to those traits are critically important so that the effects of variation in plant secondary chemistry in insects is an important area of research. Populations of *Apterothrips apterus* are affected strongly by their individual host plants with some individuals consistently supporting high densities of thrips while others are free<sup>32</sup>. An equally striking example relates to populations of *Scirtothrips dorsalis* which show striking population diversity on individual plants of four varieties of chillies, CLRT, SB, HW and CLS, essentially through variation in their alkaloid contents<sup>33</sup>. In the most preferred variety CLRT the number of adults recorded was nearly 85.6% higher compared to the least preferred CLS. The population of immatures was also high in CLRT with better potential of subsequent emergence of large adult populations establishing a significant correlation between colonization and feeding on the basis of varietal choice. As such genetic variation in resistance among plants could result in diverse patterns of herbivore community structure. Sometimes specialists and generalists tend to exhibit complimentary patterns of abundance, because characters that confer resistance to generalists could be used as attractants to specialist herbivores<sup>34</sup>.

Instances where even within a population both generalist and specialist phenotypes are maintained, are exemplified by the butterfly *Euphydras editha*<sup>28</sup>. Evidence for preference-performance correlation has been shown by offspring of specialist females surviving better on plants chosen by their mother than on rejected plants. On the other hand, offspring from generalist females performed equally well on both categories of plants. In some swallowtail butterflies, some of the genes affecting larval performance on hosts are different from the genes affecting oviposition performance. Further, several differences exist in the genetics of larval performance and adult preference in several groups of swallowtails<sup>35</sup>. Resource texture therefore is an aspect to which insects respond in various ways. In a mixed crop situation a specialist used to host specific cues might be confused or repelled by nearby non-host species, while a polyphagous generalist species may perceive diverse plant mixtures without adverse

effects. Many species use non-specific chemical cues as part of the host selection mechanism and specialists are known to be more selective than generalists to deterrents from non-hosts. By tending to lose sensitivity to chemical compounds, deterrence has been suggested to be a cause for specialization<sup>36</sup>.

A vast majority of gall-inducing insects are specialists since they are highly specific to their host plants. Host plant choice by the gall insects needs to be seen in conjunction with the phenology and quality of the plant<sup>37,38</sup>. Incidence patterns of host plant fructose and its effects are enhanced by phylloplane proline, glucose and sucrose correlate with the oviposition preference. Single non-specific compounds like inositol regulate feeding activity and foliar nitrogen enables better life history performance<sup>39,40</sup>. Insects restricted to one host plant species or a narrow range of related plants need to search and locate the most suitable host plants.

## Conclusion

Resistance variation tends to influence the evolution of several insect characters including the ability to survive and reproduce on a particular host genotype. While induced responses affect herbivore performance, the consequences of their effects on insect population dynamics as well as plant fitness and defence are aspects which need more intensive studies. Nevertheless it cannot be denied that herbivory and induced resistance are significant forces 'moulding plant fitness depending upon the effectiveness of induced resistance and tolerance of plants to herbivory'<sup>41</sup>. An understanding of the variability of induced defences in terms of phenotypic plasticity and the degree of heritability of such variations are also aspects which need attention, particularly when plant chemistry is of significance in the maintenance of narrow host ranges.

1. Ehrlich, P. R. and Raven, P. H., *Evolution*, 1964, **18**, 586-608.
2. Singer, M. C. and Parmesan, C., *Nature*, 1993, **361**, 251-253.
3. Eastop, V. F., in *Insect-Plant Relationships* (ed. Van Emden, H. F.), Blackwell Scientific Publication, London, 1973, pp. 157-178.
4. Scriber, J. M. and Ayres, M. P., *Atlas Sci. Anim. Plant. Sci.*, 1988, **1**, 117-123.
5. Feeny, P., *Recent Adv. Phytochem.*, 1976, **10**, 168-213.
6. Rhoades, D. F. and Cater, R. G., *Recent Adv. Phytochem.*, 1976, **10**, 168-213.
7. Rhoades, D. F., in *Herbivores: Their Interaction with Secondary Metabolites* (eds Rozenhal, G. A. and Janzen, D. H.), Academic Press, Orlando, 1979, pp. 3-54.
8. Herms, D. A. and Mattson, W. J., *Quart. Rev. Biol.*, 1993, **67**, 83-85.
9. Coley, P. D., *New Phytol.*, (suppl.), 1986, **106**, 251-263.
10. Coley, P. D., Bryant and Chaprin, F. S., *Science*, 1985, **230**, 895-899.
11. Schlichting, C. D. and Levin, D. A., *Ann. Rev. Ecol. Syst.*, 1986, **17**, 667-693.
12. Hartmann, T., *Ent. Exp. Appl.*, 1996, **80**, 177-188.
13. Grime, J. P., Crick, J. C. and Rincon, J. E., in *Plasticity of Plants* (eds Jennings, D. H. and Trewavas, A. J.), The Company of Biologists Ltd, Cambridge, pp. 5-29.
14. Zangerl, A. R. and Berenbaum, M. R., *Ecology*, 1993, **74**, 47-54.
15. Gottlieb, O. R., *Phytochemistry*, 1989, **28**, 2545-2558.
16. Harborne, J. B., *Biol. J. Linn. Soc.*, 1990, **39**, 135-151.
17. Stout, M. J., Workman, K. V. and Duffey, S. S., *Entomol. Exp. Appl.*, 1996, **79**, 255-271.
18. Berenbaum, M. R., *Evolution*, 1983, **37**, 163-179.
19. Berenbaum, M. R., Zangerl, A. R. and Lee, K., *Oecologia*, 1999, **80**, 501-506.
20. Berenbaum, M. R. and Neal, J. J., *J. Chem. Ecol.*, 1985, **11**, 1349-1358.
21. Dowd, P. F., *J. Chem. Ecol.*, 1989, **15**, 249-254.
22. Koul, O., Smirle, M. J., Isman, M. B. and Szeto, Y., *Experientia*, 1990, **46**, 1082-1084.
23. Ananthakrishnan, T. N., Sen, Ryan, R. and Annadurai, R., S. and Murugesan, S., *Proc. Indian Acad. Sci.*, 1990, **99**, 39-52.
24. Schoonhoven, L. M., Jermy, T. and Van Loon, J. J. A., *Insect-Plant Biology*, Chapman and Hall, London, 1998.
25. Ananthakrishnan, T. N., Gopichandran, R. and Gurusubramanian, J. *Biosci.*, 1992, **17**, 483-489.
26. Ananthakrishnan, T. N., Gopichandran, R., *Chemical Ecology in Thrips - Host Plant Interactions*, Oxford and IBH, New Delhi, 1994, p. 125.
27. Singer, M. C., in *Behavioural Mechanisms in Evolutionary Ecology* (ed. Real, L.), University of Chicago Press, 1993.
28. Thomson, J. N., *The Coevolutionary Process*, Chicago University Press, 1994, p. 376.
29. Berenbaum, M. R., *Arch. Insect Biochem. Physiol.*, 1991, **17**, 165-185.
30. Geo, B. Z., Widstrom, N. W., Wiseman, B. R., Snook, M. E., Lynch, R. E. and Plaisted, D., *J. Econ. Entomol.*, 1979, **92**, 746-753.
31. Bower, M. D. and Puttick, G. M., *J. Chem. Ecol.*, 1990, **16**, 165-185.
32. Karban, R., *Nature*, 1989, **340**, 60-61.
33. Gopichandran, R. and Ananthakrishnan, T. N., in *Biochemical Basis of Host Plant Resistance in Insects*, National Academy of Agricultural Sciences, New Delhi, 1996, pp. 65-88.
34. Simms, E. L. and Fritz, R. S., *TREE*, 1990, **5**, 356-360.
35. Bernays, E. A. and Chapman, R. F., *Mol. Entomol.*, 1987, **49**, 108-116.
36. Abrahamson, W. G. and McGrea, K. D., *Proc. Ent. Soc. Wash.*, 1986, **88**, 364-367.
37. How, S. T., Abrahamson, W. G. and Craig, F. P., *Environ. Entomol.*, 1993, **22**, 388-396.
38. Raman, A., *Int. J. Ecol. Environ. Sci.*, 1996, **22**, 133-145.
39. Derridj, S., Gregory, V., Boutin, J. P. and Fiala, V., *Entomol. Exp. Appl.*, 1989, **53**, 267-276.
40. Minckenberg, O. P. J. M. and Fredrix, M. J., *J. Ann. Entomol. Soc. Amer.*, 1989, **82**, 350-354.
41. Karban, R. and Baldwin, I. T., *Induced Responses to Herbivory*, The University of Chicago Press, 1997, p. 318.

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