

16. ISRO-SP-03-94, Liquid Propellant Rocket Engines, Library and Documentation Centre, Shar Centre, 1994.
17. Air & Cosmos no. 1421, Trente Ans de Missiles Balistiques Strategiques Rusees, 12-18 April 1993.
18. The inert weight to propellant weight ratio is governed by engineering considerations that include material and fabrication capabilities. Scale economies related to the size of the engine and stage also play a part in determining this ratio. For the *Ghauri* kind of engine and stage, expert opinion was sought to assess the veracity of the data put out in published sources after the *Ghauri* launch. Experts familiar with the design of similar liquid rocket stages and engines were of the opinion that the inert weight to propellant ratio of 0.1538 was realizable and realistic given the material and fabrication capabilities of countries like Pakistan or North Korea.
19. Robert. S. Norris *et al.*, *Nuclear Weapons Databook*, vol. V, Westview Press.
20. See ref. 7.
21. See ref. 8.
22. See ref. 17.
23. The images used for the analysis are from refs 4 and 5.
24. George P. Sutton, *Rocket Propulsion Elements*, 6th edition, Wiley Interscience Publications, p. 217.
25. See Country briefings in the CDISS website <http://www.cdiss.org>.
26. See assessment by C.Vick in the Federation of American Scientists website at <http://www.fas.org>.
27. Air & Cosmos no.1421, Trente Ans de Missiles Balistiques Strategiques Rusees, 12-18 April 1993.
28. For e.g. a report on the North Korean link of the *Ghauri* was carried by *The Hindu* on 2 May 1998. Either by coincidence or by intent, the US imposed sanctions on a Pakistan laboratory almost immediately. *The Hindu*, 2 May 1998.
29. Chidanand Rajghatta, *Indian Express*, 5 May 1998.
30. See ref. 3.
31. See ref. 4.
32. See for e.g. Khergamvalla, F. J., *The Hindu*, 20 September 1998.
33. There is no confirmation from US official sources that a satellite was put into orbit. Other sources especially Russian believe that something was put into orbit. The most authentic source for tracking satellites put into orbit is the data put out by the North American Defence Command (NORAD). NORAD maintains an open web site, which lists current launchings and updates orbital elements for objects in orbit around the earth. The NORAD listings do not include a North Korean satellite as of 26 November 1998. The NORAD web site can be accessed at <http://celestrak.com/NORAD/elements/index/html>.
34. Jonathan McDowell from the Harvard Smithsonian Centre for Astrophysics runs a weekly service that reports on and provides updates on various launchings around the world. These reports are based not only on sources from NORAD but also other sources and contacts around the world. Weekly reports nos 371, 372 and 373 deal with the North Korean satellite/failed missile launching. Jonathan McDowell's weekly reports of space launchings can be accessed at <http://hea-www.harvard.edu/~jcm/space/jsr/jsr.html>.

ACKNOWLEDGEMENTS. I thank Shri Gopal Raj, Science Correspondent of *The Hindu* for very useful discussions and inputs. Shri Sivaramakrishnan Nair formerly from ISRO was of great help in answering and clarifying a number of technical issues that came up during this work. I also thank many of my current and former colleagues from ISRO whose readiness to share their expertise contributed in no small measure to this article. This assessment is as much their effort as mine. I would also like to thank Shri K. P. Basvarajappa of the Indian Institute of Management, Bangalore for his help with this article.

Received 8 October 1998; revised accepted 10 December 1998

## Induced responses, signal diversity and plant defense: Implications in insect phytophagy

T. N. Ananthakrishnan

*Damage to plant tissues due to insect feeding induces diverse biochemical and physiological processes generating at the feeding site, signals which move through the plant, eliciting induced responses. Both primary and secondary metabolites change following damage, resulting in changing profiles of allelochemicals. The damaged plant tissues respond in diverse ways, plant signal transduction involving communication within the plant of the concerned responses. Of particular relevance are the proteinase inhibitors which have the potential to contribute towards plant defense against insects, as also of a host of secondary chemicals which differ with different plants. Manipulation of induced plant defense in the regulation and stimulation of natural enemies involving characteristic volatiles emitted by infested plants is also discussed, besides the possible role of induced defenses in pest management.*

CHANGES in plant function induced by insect feeding involve consideration of changes in resistance in terms of biochemical, physiological and morphological aspects

which tend to alter plant growth, reproduction and storage, restricting, retarding or overcoming further damage essentially through eliciting diverse behavioural chemical stimuli resulting from induction. While constitutive defenses are always expressed in the plant, induced responses following insect damage enable a

T. N. Ananthakrishnan lives at 'Rainapriya', 18, Pushpa Nagar, 1st Street, Nugambakkam, Chennai 600 034, India.

better assessment of the defense systems of the plants which tend to restrict the host plant preferences, insect survival and reproductive efficiency. Damage to the plant tissue due to insect feeding leads to the translocation of a signal from the damaged site to other parts of a plant resulting in induced resistance, the expression of which tends to vary with the age, season and growth habits. Since the damaged plant tissues respond in diverse ways with many of the responses occurring away from the site of damage, the terms talking or listening plants were often used. The responses may be either short term and rapid or long term and delayed, the former tending to be more effective against generalist insects and the latter against both generalist and specialist insects<sup>1</sup>. While qualitative or mobile defenses are easily translocated among plant tissues, the same is not true of quantitative or immobile defenses<sup>2</sup>. Induced defenses tend to be more effective against unpredictable herbivores than constitutive defenses<sup>3</sup>.

The pioneering contributions of the biochemist Clarence Ryan and the Finnish Ecologist Haukioja laid the foundation for some intensive studies in induced resistance against herbivores. Rapid accumulation of proteinase inhibitors as a result of feeding by *Leptinotarsa decimlineata*<sup>4</sup> and the response of birches to defoliation by the larch bud moth producing heavily-defended foliage causing crash of caterpillars<sup>5-7</sup> are notable examples. A correlation of population dynamics of the concerned insects with the defense chemicals released by the plant after damage, is an essential aspect, the response generally depending on the concentration of chemicals<sup>8</sup>. Some of the best examples of rapidly inducible phytochemical responses are the increase of cucurbitacins in the attacked leaves of cucurbits and nicotine production in tobacco, and the production of diverse furano-coumarins as a result of feeding by danaiid caterpillars on umbellifers<sup>9</sup>. Of equal interest is the emission by disturbed foliage of eucalyptus species, of isoprene,  $\alpha$ -pinene, cineole, limonene and  $\beta$ -terpene, while undisturbed leaves released only isoprene, adequately demonstrating thereby that induced chemical responses tend to reduce plant attractiveness to herbivores<sup>10</sup>. Plant structures as such are arenas for the competitive interactions of the insect species exploiting them, phytophagous insects always exerting a selective pressure that promotes diversification of defense mechanisms in plants<sup>11</sup>.

### Signal diversity and nature of responses

The nature of the signals involved in the recognition of damaged plant tissues and conveyance of the information to other parts of the plant, form basic tenets of the induced responses. Different plants which use different signals and diverse biochemical and physiological processes which result in induced resistance are

chains of multiple reactions which involve many different compounds<sup>12</sup>. Such signals, which are generated rapidly in the plants at the site of insect damage, travel through the plants eliciting the induced response which follows a time course. While diverse signals are used by different plants and different kinds of damage may result in the eliciting of different signals in the same plant, the possibility of a single plant using more than one mode of signaling also exists. Not only have the plant signals generated increased interest in relation to induced plant responses, knowledge of the cues and signals is useful in experimental induction of resistance in crop plants. It has also been reported that the speed of induction also plays a role in the effectiveness of the induced responses<sup>13</sup>. Further changes in the secondary chemicals are in many cases induced in all the leaves above a certain threshold of damage, so that the plant subsequently becomes more resistant to insects. Where no such threshold exists, even a minor damage may result in changes in the leaf chemistry which subsequently results in the insect moving away from the site of damage<sup>14</sup>. Coleman and Jones<sup>15</sup> have produced a 'phyto-centric model' for interpreting insect-induced changes in resource quality and the suitability of plant tissues in the light of other factors influencing plant functions. The model highlights the biochemical or physiological characters which determine the quality of plant resources resulting from resource acquisition, allocation and partitioning.

Plants respond to physical and chemical changes associated with insect feeding, through the accumulation of phenolic compounds and in accordance with the kind and degree of damage, diverse phenols are induced which involve enzymes such as phenylalanine ammonia lyase (PAL), tyrosine ammonia lyase (TAL), polyphenol oxidases (PPO) and peroxidases (PO). While PAL activity is stimulated differentially in accordance with the insect damage, the enzyme is also known to exist in multiple forms which are induced differently by different cues. Most of the higher plant polyphenols are produced through the intermediation of phenylalanine which involves multienzyme complexes including PAL. The number of genes coding for PAL also varies differentially and each of these tends to produce varying amounts of the enzyme. A signal passes from the site of damage to undamaged leaves inducing PAL activation<sup>12,16</sup>. Other enzymes have also been observed to be produced differentially by different elicitors. It is well known today that a local stimulus triggers signaling effects that affects the whole plant.

Defense responses induced by elicitors relate to biochemical and molecular mechanisms, of which proteinase inhibitors are well known. Serine proteinase inhibitors have been well investigated as markers for systemic wound responses in tomato and potato plants and are

expressed in the aerial regions of the plants. Increased exposure to proteinase inhibitors have a detrimental effect on the digestive physiology of several larval Lepidoptera<sup>17,18</sup>. The polypeptide systemin produced close to the damage sites of plants acts as a plant hormone inducing proteinase inhibitors<sup>19</sup>. Systemin released by wounding, translocates throughout the plant and interacts with the distal tissues of plants where it stimulates synthesis of jasmonic acid which activates proteinase inhibitor genes. Responses to proteinase inhibitors by insects involve production of proteases which result in degradation of essential amino acids. Synthesis of diverse plant proteins believed to be of importance in defense is also known<sup>20</sup>. Treatment with methyl jasmonate induces accumulation of other chemicals involved in plant defense such as ethylene, PAL, systemin and several alkaloids. Both short-distance and long-distance signal pathways are thought to activate proteinase inhibitor genes by means of a secondary signal pathway, the octadecenoid pathway<sup>21</sup> which results in the synthesis of jasmonic acid and methyl jasmonate, which are known to elicit different chemical and physiological responses and provide a potential mechanism for communication in or between plants<sup>22</sup>.

Feeding damage by thrips enhances production of ethylene which in turn is known to enhance production of defense chemicals. Plant phenolic levels increase in response to ethylene and initiates PAL activity. While oligosaccharide fragments of cells are known to act as systemic signals producing rapid induction of proteinase inhibitors, ethylene results in the production of enzymes that release these oligosaccharide fragments. Similarly abscissic acid acts as a signal for induced accumulation of proteinase inhibitors. Methyl salicylate found in the wounded plant tissues induces production of a variety of chemicals involved in plant defense. Thus an intensive network of signals is mobilized through the activation of local systemic events. The diversity of such local signals arising from tissue damage which lead to systemic changes in gene expression are areas of future research.

### Allelochemical diversity in induced defense

Involvement of changes in age-correlated chemistry of plant growth and development as well as the impact of physicochemical induction results in changing profiles of allelochemicals which modify the behaviour of natural enemies. Increasing number of cultivars of crop plants naturally call for more intensive studies on their chemodynamics in order to establish the nature of their resistance to pests. While plant resource acquisition, allocation and partitioning are basic processes which determine the suitability of plants to insects, the more recent view that the increasing chemical diversity in plants is due to the additive effects of synergistic interactions as a

form of multichannel defenses, has further emphasized the need for a proper appreciation of induced defenses. Although host suitability can be a function of structural, physiological or habitat characters associated with the plant, allelochemicals, whether constitutive or induced, are the major determinants of host suitability. While induced responses may be selected secondarily as protection against herbivores, there is growing evidence that their induction may be in response to resource allocation or carbon/nutrient balance<sup>23-25</sup>.

As fitness of plants is also associated with primary as well as secondary metabolites, an assessment of plant chemical defense also depends on the interaction between, say dietary protein of insects as well as chemical defenses of plants in cases where detoxification enzymes are substrate-based<sup>26</sup>.

Induced resistance against many insects and mites resulting from plant growth regulators and hormones lead to increased accumulation of secondary chemicals. Chlormequat chloride, a plant growth regulator, has been known to induce resistance against many insects such as aphids with the production of increased levels of plant pectins and methoxypectin which interfere with insect feeding<sup>27,28</sup>. Of equal interest is the sunflower damage by *Zygogramma* and the flower thrips which induce production of hydroxycoumarin and methylene dioxycoumarin which deter further feeding and the profiles of coumarins tend to vary.

Increasing instances are evident in several insect-plant systems wherein induced defenses play a useful role. Damage caused by insects can induce production of tissue-based phenols, and additional compounds tend to be produced over a longer period. Continued attack by flea beetles on crucifers can change the total concentration of glucosinolates in different plant tissues leading to a 2- to 4-fold increased production of glucosinolate such as glucobrassicin and neoglucobrassicin<sup>29</sup>. When the plant tissues are disrupted, the enzyme myrosinase hydrolyses the glucosinolate to produce a variety of products collectively called mustard oils<sup>30</sup>. Similarly allyldisulphide and propyldisulphide of onion are released from the bound form in the plants especially after its damage<sup>31</sup>. The speed and intensity of biosynthesis of these chemicals may depend on the distance from the site of injury, amount of damage done and the kind of elicitors involved. Feeding by insects also induces phytoalexins which are antimicrobials, while in cases like feeding by gall mites, accumulation of chitinases and gluconases results<sup>32</sup>. It is now firmly believed that most herbivores carry microbes to the damaged site, and phytoalexin production is a component of the plants response to herbivory. Different classes of phytoalexins are produced by different families such as isoflavanoids in the Leguminosae. These phytoalexins have been ascribed a role in plant disease resistance.

Resistant cultivars of cotton evincing increased PAL, TAL enzymes when attacked by *Helicoverpa armigera* result in increased production of gallic, salicylic acids, besides resorcinol and phloroglucinol<sup>33</sup>. A significant shift in the oxidative status of the host plants is typical of induced resistance, and several oxidative enzymes are induced in *Heliothis zea*. Increased levels of syringic acid, chlorogenic acid, ferrulic acid, and rutin resulted in foliage fed by *H. zea*. A significant decline was also seen in the host nutritional quality with decrease of most amino acids in the damaged tissue. Induced resistance also involves lignification and cell wall strengthening, increased lignification resulting from changes in ferrulic and *p*-coumaric acid levels in damaged squares. Inhibition of damage-induced ethylene synthesis is associated with increased ferrulic acid in foliage<sup>34</sup>.

Multiple stem galling of several cotton cultivars by the cotton stem weevil *Pempherulus affinis* revealed increased inputs of some of the above allelochemicals, as against ungalled stems which showed pyrogallol and to a little extent hydrobenzoic acid. Increasing trend in gossypol and tannin content was also evident with the increased onset of galling<sup>35</sup>.

### Impact of induction on tritrophic interactions

Plants have evolved to use parasites and predators as a defense against phytophagous insects, phytochemicals of the host plants acting as long range cues for attracting natural enemies. Variation in plant traits whether physical, morphological or chemical can affect the fitness of natural enemies. Effects of induced responses on natural enemies may also act additively or synergistically as is evident from the prolonged development of insect larvae-induced allelochemicals arresting or reducing growth, thereby attracting natural enemies which have evolved the capability to learn to use induced responses for host location. Thus plants use the third trophic levels as another line of defense against herbivores. To be more effective there should be stronger selection pressure on plants to release chemical signals that attract natural enemies. Besides the release of volatile chemicals, herbivory may change non-volatile allelochemicals which may further increase natural enemy activity. The emission of volatiles can be adaptive to plants when they attract natural enemies that reduce herbivore damage, the volatiles enhancing the foraging efficiency of natural enemies<sup>36</sup>.

It is well known that  $\beta$ -glucosidase is an effective elicitor<sup>36</sup> of herbivore-induced plant odour which attracts parasitic wasps.  $\beta$ -glucosidase is found in the regurgitated saliva of caterpillars. Being an elicitor of defense responses to herbivore injury it induces the emission of volatiles used by natural enemies to locate their victims. Herbivore-induced plant volatiles may provide natural

enemies with the information about plant species and they are more reliable than general damage related plant volatiles. Release of green leaf volatiles in damaged plants includes a mixture of C6 alcohols, aldehydes and esters and these volatiles by diffusing through the air produce behavioural responses.

One of the best examples of tritrophic systems relates to the lima bean plant and the two spotted mite *Tetranychus urticae* and the predatory mite, *Phytoseiulus persimilis*<sup>37</sup>. Similarly herbivore-induced plant synomones are beneficial to the signaler (plant) and the receiver (natural enemy) as in the case of some anthocorids which were attracted to pear trees infested by the pear psyllid<sup>38</sup>.

The conducive niche offered by squares and flowers of cotton provides pollen and other nutritional sources to natural enemies, not to mention the kairomonal compounds such as eicosane, pentacosane and dodecenoic acid in plant sources tending to adequately increase the activity of natural enemies in a variety of crops<sup>39</sup>. Release of plant volatiles after feeding by phytophagous insects increases the fitness of the entomophagous insects especially through such volatile fractions as caryophyllene, hexanoic, tetradecenoic, hexadecenoic and pentadecenoic acids, which also emanate from larval frass and larval cuticle resulting from feeding on different plant sources, appreciably attracting natural enemies<sup>40</sup>. Turlings *et al.*<sup>41</sup> have shown that partly damaged leaves by *Spodoptera exigua* release terpenoids such as  $\alpha$ -transbergamotene, (E)- $\beta$ -farnesene and (E)-nerolidol. Similarly cotton seedlings produce volatiles cues when infested with herbivorous mites and elicit attraction of predatory mites<sup>43</sup>. Volatile chemicals from host plants, host insects or frass are informational cues which augment the activity of larval parasites such as *Microplitis croceipes*.

### Induced resistance in pest management

Breeding programmes for crops could select plants with high levels of induced resistance against insects (as also against bacterial, fungal and viral infection)<sup>43</sup>. Insufficient cognizance of the chemodynamics of insects has often been a major cause for not achieving anticipated levels of pest management. Prospects for genetically engineered crops are exciting because resistance traits can be fused to promoters so that they can be made to express following attack.

Application of bioregulators tends to induce chemical changes in plants, resulting in higher concentration of allelochemicals and reduced nutritional inputs. Crop plants could be bred for more induced resistance and genes could be added by genetic engineering providing induced resistance in crop genomes<sup>44</sup>. Since genes can be transferred among plants of different species, there are

increased possibilities of crop improvement through genetic engineering. With the proper knowledge of the mechanisms of induced resistance the possibility of adding such resistant genes to plants which do not have them are great, particularly in view of the availability of vectors to incorporate foreign genes into the genomes of plants. To date plants have only been transformed with a few gene products for potential defense against herbivory, as for instance systemin, proteinase inhibitors and Bt endotoxins. One of the best examples relate to fusing the gene that produces Bt endotoxins to a promoter that activates it only after the plant has been damaged<sup>45</sup>. Similarly proteinase inhibitor genes are also wound-inducible, enabling expression of the inhibitor only after the plants are damaged. Initial encouragement received from systemin, proteinase and  $\alpha$ -amylase inhibitors and Bt endotoxin-induced resistance in genetically engineered crops have sufficiently added to their potential in pest management, besides the prolongation of the usefulness of the transgenics.

## Conclusion

Much of the chemical profile of a plant is altered following phytophagy including plant secondary metabolites which tend to have deterrent or antibiotic effects on insects. Phytophagy and induced-resistance to insects are prone to be important aspects promoting plant fitness which depends on the effectiveness of the induced responses and the degree of resistance of plant to insect damage. The responses to wounding activated by the plants signal transduction pathway considerably influence feeding by the concerned insects. Oligosaccharide fragments from plant cell walls, systemin, salicylic acid, ethylene, abscissic acid, jasmonic acids are implicated as signals in systemic induction and being of the nature of signals a chemical must be necessary to induce the observed responses. Gallic and salicylic acids are known to play an important role in insect-plant and plant-pathogen interactions. Salicylic acid besides activating as a defensive chemical also acts as a signal which moves through the plant, having the attributes of a plant hormone<sup>46</sup>. Plants are therefore to be considered as a dynamic component of insect-plant interactions. Secondary metabolites cannot be manipulated using transgenesis in view of the complicated biosynthetic reactions which require several enzyme-mediated steps. While plant-insect interactions result in marked changes in plant secondary chemicals, nutrient status and physiology, which might affect subsequent resistance to herbivores, there is also a need to examine the possible impact of pathogens in this process to be able to confidently conclude regarding the specificity of induced defenses. An equally important aspect relates to the need for more intensive studies on the diversity of induced responses

on insects to appreciate the useful application of such responses in plants.

1. Rhoades, D. F., in *Herbivores: Their Interaction with Secondary Plant Metabolites* (eds Rosenthal, G. A. and Janzen, D. H.), New York Academic Press, 1979, pp. 3-54.
2. Coley, P. D., Bryant, J. P. and Chapin, T., *Science*, 1985, **22**, 895-899.
3. Faeth, S. H., in *Parasitoid Community Ecology* (eds Hawkins, B. A. and Sheehan, W.), Oxford University Press, Oxford, 1994, pp. 245-260.
4. Green, T. R. and Ryan, C. A., *Science*, 1972, **175**, 776-777.
5. Haukioja, E., *Oikos*, 1982, **35**, 202-213.
6. Haukioja, E., *Annu. Rev. Entomol.*, 1990, **36**, 25-42.
7. Haukioja, E. and Niemala, P., *Ann. Zool. Fennici*, 1990, **14**, 25-42.
8. Myers, J. H., in *Chemical Mediation of Coevolution* (ed. Spencer, K. C.), Academic Press, Sandiego, 1988, pp. 345-365.
9. Berenbaum, M., *Ecology*, 1981, **62**, 1254-1266.
10. Rhoades, D. F., *Am. Nat.*, 1985, **125**, 205-238.
11. Zwolfer, H., Proceedings of the 5th International Symposium, Pudoc, Wagenmgen, 1982, pp. 287-296.
12. Karban, R. and Baldwin, I. T., in *Induced Responses to Herbivory*, The University of Chicago Press, Chicago, 1997, pp. 319.
13. Baldwin, I. T. and Schmelz, E. A., *Ecology*, 1996, **77**, 236-246.
14. Edwards, P. J., Wratter, S. D. and Gibberd, R. M., in *Phytochemical Induction by Herbivores* (eds Tallamy, D. W. and Raupp, M. J.), John Wiley, New York, 1991, pp. 205-221.
15. Coleman, J. S. and Jones, C. G., in *Phytochemical Induction by Herbivores* (eds Tallamy, D. W. and Raupp, M. J.), John Wiley, New York, 1991, pp. 3-45.
16. Hartley, S. E. and Lawton, J. H., in *Phytochemical Induction by Herbivores* (eds Tallamy, D. W. and Raupp, M. J.), John Wiley, New York, 1991, pp. 105-132.
17. Broadway, R. M. and Duffey, S. S., *J. Insect Physiol.*, 1986, **32**, 827-833.
18. Broadway, R. M., Duffey, S. S., Pearce, G. and Ryan, C. A., *Entomol. Exp. Appl.*, 1986, **41**, 33-38.
19. Pearce, G. D., Strydom, D., Johnson, S. and Ryan, C. A., *Science*, 1991, **253**, 895-898.
20. Reinbothe, S., Mollenhauer, B. and Reinbothe, C., *Plant Cell*, 1994, **6**, 1197-1209.
21. Costebel, C. P., Bergey, D. R. and Ryan, C. A., *Proc. Natl. Acad. Sci. USA*, 1995, **92**, 407-411.
22. Farmer, E. E. and Ryan, C. A., *Proc. Natl. Acad. Sci. USA*, 1990, **92**, 7713-7716.
23. Bryant, J. P., Tourni, J. and Niemala, P., in *Chemical Mediation of Coevolution* (ed. Spencer, K. C.), Academic Press, Sandiego, 1988, pp. 367-389.
24. Toumi, J., Niemala, P., Haukioja, E. et al., *Oecologia*, 1984, **61**, 208-210.
25. Toumi, J., Hagerstrom, T. and Niemala, P., in *Phytochemical Induction by Herbivores* (eds Tallamy, D. W. and Raupp, M. J.), John Wiley, New York, 1991, pp. 85-104.
26. Johnson, N. D. and Bentley, B. L., *J. Chem. Ecol.*, 1988, **14**, 1391-1403.
27. Dreyer, D. L., Campell, B. C. and Jones, K. C., *Phytochemistry*, 1984, **23**, 1593-1596.
28. Fisher, D. C., Kogan, M. and Greamy, P., in *Safer Insecticides: Development and Use* (eds Hodgson, E. and Kuhr, R. J.), Marcel Dekker, New York, 1990, pp. 257-280.
29. Renwick, J. A. A., Radke, C. D. and Sachedev-Gupta, K., *Chemoecology*, 1992, **3**, 33-38.
30. Bennet, R. N. and Wallsgrave, R. M., *New Phytol.*, 1994, **127**, 617-633.
31. Bernays, E. A. and Chapman, R. F., *Host Plants Selection by Phytophagous Insects*, Chapman and Hall, London, 1994.

32. Bronner, R., Westphal, E. and Dreger, F., *Physiol. Mol. Plant Pathol.*, 1991, 38, 93-104.
33. Ananthakrishnan, T. N., Sen Rayan, R., Annadurai, R. S. and Murugesan, S., *Proc. Indian Acad. Sci.*, 1990, 99, 39-52.
34. Bi, J. L., Murphy, J. B. and Felton, G. W., *J. Chem. Ecol.*, 1997, 23, 97-117.
35. Prakash, D. S., Ph D thesis, University of Madras, 1997.
36. Mattiacci, L., Dicke, M. and Posthumus, M. A., *Proc. Natl. Acad. Sci. USA*, 1995, 92, 2036-2040.
37. Karban, K. and Baldwin, I. T., *Induced Responses to Herbivory*, University of Chicago Press, 1997, pp. 319.
38. Vet, L. E. M. and Dicke, M., *Annu. Rev. Entomol.*, 1992, 37, 141-172.
39. Annadurai, R. S., Murugesan, S. and Sen Rayan, R., *Proc. Indian Acad. Sci.*, 1990, 99, 317-325.
40. Ananthakrishnan, T. N. and Sen Rayan, R., *Phytophaga*, 1992, 4, 87-94.
41. Turlings, T. C. J., Tumlinson, J. H. and Lewis, W. J., *Science*, 1990, 250, 1251-1253.
42. Bruin, J., Dicke, M. and Sabelis, M. W., *Experientia*, 1992, 48, 525-529.
43. Kogan, M. and Paxton, J., in *Plant Resistance to Insects* (ed. Hedin, P. A.), ACS, Washington DC, 1983, pp. 153-171.
44. Ryal, S. J. E., Ward, P., Ahl-Goy and Metraux, J. P., in *Induced Plant Proteins* (ed. Wray, J. L.), Cambridge University Press, 1992, pp. 205-229.
45. Ryan, C. A., *Bioessays*, 1989, 10, 20-24.
46. Ananthakrishnan, T. N., *Curr. Sci.*, 1997, 73, 576-579.

Received 16 May 1998; revised accepted 3 December 1998

## Evolution of saline lakes in Rajasthan

A. B. Roy

*Saline lakes are widely distributed in the Thar desert of western Rajasthan. The cardinal factors in the evolution of saline lakes are aridity and the formation of playa depressions, characterized by ephemeral drainage of centripetal type. Most of the large saline lakes are found to have riverine ancestry. Common models suggested for the evolution of saline lakes involve segmentation of stream channels with the onset of aridity. Stream trapping phenomenon is associated with a few saline lakes. The most effective process of stream segmentation was through the formation of linear horsts across the NE-SW trending river channels. Integrated studies based on geophysical, tectonic and remote sensing data indicated control of NE-SW and NW-SE intersecting sets of lineament, particularly the nature of movement along them, in the development of playa depressions. The process of formation of saline lakes can be tied up with the blotting out of the Saraswati and Drishadvati river systems due to drainage disorganization during the Late Quaternary.*

The saline lakes are as much a part of the desert landscape as the sand dunes are. Both the features develop under the conditions of aridity. While the sand dunes form through aeolian process, involving wind action, the major constraint for the evolution of saline lakes is the low to very low precipitation with correspondingly very high rate of evaporation. The saline lakes are widely distributed in the arid western Rajasthan. A few saline lakes, including the Sambhar, the largest one, occur right on the Aravalli mountains. Besides the Sambhar, other important saline lakes are at Didwana, Lunkaransar, Kuchaman, Pachpadra (Panchbhadra), Pokaran, Chhapar, Thob and other places in the plains of the Thar Desert (Figure 1). In addition to these large lakes, there are many smaller saline depressions which occur between the sand dunes. A characteristic feature of most saline lakes in Rajasthan is the NE-SW trend of their longer axis. Topographically, the saline lakes

occupy the most depressed part of the isolated basins. Another characteristic feature of the saline lakes is the centripetal drainage system of ephemeral type (Figure 2).

Aridity being the prime factor in the development of saline lakes, it may be pertinent to inquire when actually such a condition had set in. Some crucial information is now available on the time of setting of aridity in western Rajasthan. Thermoluminescence dating of ancient sands in the region suggests that the arid condition prevailed here at least since 1,50,000 years before the present<sup>1</sup>. Detailed sedimentological studies of the Sambhar, Didwana and Lunkaransar lake deposits, however, furnished evidence of transition from extremely arid to sub-humid and wet regimes during the period mentioned above<sup>2-7</sup>.

### Origin of saline lakes

Several theories have been proposed in the past to explain the salinity as well as the origin of saline lakes

A. B. Roy is in the Department of Geology, Mohanlal Sukhadia University, Udaipur 313 002, India.