

A REVIEW :

Plant lectins and their insecticidal potential

■ YARASI BHARATHI

ARTICLE CHRONICLE :

Received :

15.07.2017;

Accepted :

30.07.2017

SUMMARY : Lectins are a group of sugar-binding proteins that recognize specific carbohydrate structures and agglutinate a variety of animal cells by binding to cell-surface glycoproteins and glycolipids. Many biological processes in nature are triggered and nurtured by protein carbohydrate recognition and protein-protein interactions. Lectins mediate cell-cell and host-pathogen interactions through the specific recognition of carbohydrates present on the cell surface. As they occur in all classes and families of organisms, significant amounts of lectins are contained in most foodstuffs. Moreover, lectins are generally resistant to heat denaturation and gut proteolysis, and thereby affect the entire digestive tract and its bacterial population, thus have an impact on body metabolism and health. Consequently, lectins are important physiologically active ingredients and a source of potent exogenous biological signals in the diet.

How to cite this article : Bharathi, Yarasi (2017). Plant lectins and their insecticidal potential. *Agric. Update*, 12(TECHSEAR-5) : 1465-1474; DOI: 10.15740/HAS/AU/12.TECHSEAR(5)2017/1465-1474.

KEY WORDS :

Plant lectins,
Merolectins,
Hololectins

BACKGROUND AND OBJECTIVES

Lectins :

Stillmark in 1888 while investigating the toxic effects of castor bean extract (*Ricinus communis*) on blood noticed that the red blood cells (RBCs) are agglutinated, the phenomenon named as hemagglutination. A toxic protein from castor beans called “ricin” capable of agglutinating the RBCs of human and animals was identified (Stillmark, 1888). Initially the ‘agglutinins’ were found only in plants. Later when they were found in other organisms and agglutinating cells other than erythrocytes the term “lectin” (from Latin verb ‘legere’ means ‘to choose’) was proposed by William Boyd (Boyd and Slapeigh, 1954). Lectins are defined as proteins or

glycoproteins of non-immune origin with one or more binding sites per subunit, which can reversibly bind to specific sugar segments through hydrogen bonds and Van Der Waals interactions (Lis and Sharon, 1998).

Lectins are classified according to the overall structure of the primary gene translation products (Peumans and Van Damme, 1999). They are:

Merolectins:

Merolectins are monovalent, have a single carbohydrate binding domain, hence do not precipitate glycoconjugates or agglutinate cells.

Hololectins :

Hololectins are composed of at least two

Author for correspondence :

YARASI BHARATHI
Regional Sugarcane and
Rice Research Station
(PJ TSAU), RUDRUR
(TELANGANA) INDIA

carbohydrate binding domains, identical or homologous, and bind structurally similar sugar(s). Hololectins agglutinate cells and/or precipitate glycoconjugates owing to their multiple binding sites. Most of the plant lectins belong to this group.

Chimerolectins:

Chimerolectins are fusion proteins comprising of one or more carbohydrate binding domain (s) arrayed in tandem with an unrelated domain. The unrelated domain can have well defined biological activity and functions independent of the carbohydrate binding domain. Chimerolectins can behave as merolectins or hololectins depending upon the number of carbohydrate binding domains.

Superlectins:

Superlectins are also fusion proteins having two carbohydrate binding domains, arranged in tandem, but differ in terms of structure and specificity.

Plant lectins :

Classification based on sequence and three-dimensional structure :

The plant lectins are a heterogeneous group of carbohydrate binding proteins which differ in their molecular structure and carbohydrate binding specificity. They are found in seeds and in other tissues such as leaves, bark, stems, rhizomes, bulbs, tubers, etc. Because of the broad distribution and ease of isolation, plant lectins are the largest and the best characterized group among lectins. They occur in many species belonging to different taxonomic groups but are not so ubiquitous. Lectins have been identified in less than 500 plant species which belong to a small number of plant families. Rarely, lectins that differ in their sugar specificity have been found in the same plant, especially in the case of legumes and Graminae. At present seven distinct lectin families have been identified on the basis of protein sequences (Peumans and Van Damme, 1999). Although plant lectins are considered a very complex and heterogeneous group of proteins at the biochemical/ physico-chemical viewpoint, sequence, structural information and molecular cloning of lectin genes enable subdivision of plant lectins into seven families of structurally and evolutionary related proteins:

Legume lectins :

The term 'legume lectin' refers to proteins that are structurally and evolutionary related to a well-defined type of lectin that was originally discovered in seeds of legumes (Fabaceae) like jack bean, common bean, pea, peanut and soybean. The isolation and cloning of structurally and evolutionary closely related agglutinins from leaves of *Glechoma hederacea* demonstrated that related lectins also occur in the family Laminaceae. The family of legume lectins (from both Fabaceae and Laminaceae species) is fairly homogeneous as far as the molecular structure of the native lectin is concerned. These lectins composed of subunits of approximately 30kDa. These lectins are present in several hundreds of species of legumes. Many of them have been purified and characterized with respect to their molecular structure, sugar binding specificity and biological role. Around 50 of them have been sequenced, mostly by protein sequencing method (Peumans and Van Damme; 1999). These legume lectins share extensive sequence homology and three dimensional structural similarities but differ in carbohydrate specificity (Rouge *et al.*, 1991 and Sharon and Lis, 1990).

Monocot mannose-binding (bulb) lectins:

Bulb lectins are present in families such as Amaryllidaceae, Alliaceae, Araceae, Orchidaceae, Liliaceae and Bromeliaceae (Van Damme *et al.*, 1998). They are detected in various vegetative tissues but not in seeds. Monocot mannose-binding lectins, as the name indicates, exhibit exclusive specificity towards α -D-mannose. They share high similarity in sequence and overall structure (Barre *et al.*, 1996 and Van Damme *et al.*, 1987). In 1987 a lectin with exclusive specificity towards mannose (Man) was isolated and characterized in snowdrop (*Gallanthus nivalis*) bulbs (Van Damme *et al.*, 1987). This group of lectins was originally referred to as the 'monocot mannose-binding lectins' (Van Damme *et al.*, 1998). Similar type of lectins have been identified in plants other than Liliopsida (e.g., liverwort, *Marchantia polymorpha*: Peumans *et al.*, 2002) as well as in bacteria and animals. Therefore this group of lectins now referred to as 'GNA-related lectins after the first identified member.

Cereal or chitin binding lectins composed of hevein domains :

The name 'hevein' refers to a chitin-binding

polypeptide of 43 amino acids found in the latex of *Hevea brasiliensis* (rubber tree) (Waljuno *et al.*, 1975). Many plant proteins owe their chitin-binding activity to the presence of one or more hevein domains. However it was shown that various lectins with hevein domains also have high affinity for N-glycosylated animal glycoproteins (Goldstein and Poretz, 1986). This group of lectins are wide spread and occur both in monocotyledonous [e.g., wheat germ agglutinin (WGA)] as well as dicotyledonous (e.g., potato lectin) plant species.

The legume and cucurbitaceae phloem lectins also bind chitin but lack the hevein domain and have no sequence similarity with chitin-binding lectins possessing hevein domain. The chitin-binding lectins belong to the class of merolectins, hololectins and chimerolectins. Hitherto the presence of chitin-binding lectins have been observed in Gramineae, Solanaceae, Phytolaccaceae, Urticaceae, Papavaraceae and Viscaceae (Peumans *et al.*, 1996 and Raikhel *et al.*, 1993) indicating their occurrence in both monocots and dicots. They are found in seeds as well as in other vegetative tissues. The lectins of Graminae are the best characterized chitin-binding seed lectins. These lectins exhibit a marked specificity towards GlcNAc and GalNAc -oligomers but they also bind sialic acid. All Gramineae seed lectins are dimeric proteins composed of identical or similar protomers of around 17 kDa size. Wheat germ agglutinin (WGA), a representative member of chitin-binding lectins family, exists in three isoforms (WGA1, WGA2, WGA3) that differ in 5-8 amino acid residues out of a total of 171 residues in the polypeptide chain (Smith and Raikhel, 1989).

Jacalins:

The family of jacalin-related lectins comprises all proteins with one or more domains that are structurally equivalent to jacalin, a galactoside-binding lectin from jack fruit seeds (*Artocarpus integrifolia*) (Sastry *et al.*, 1986). The family of jacalin-related lectins was subdivided into two subfamilies with a distinct specificity and molecular structure. The galactose (Gal)-specific jacalin-related lectins are built up of four cleaved protomers comprising a small (β : 20 amino acid residues) and a large (α : 133 amino acid residues) sub unit and exhibit a clear preference for galactose over mannose (Bourne *et al.*, 2002). In contrast, mannose-specific jacalin-related lectins are built up of uncleaved protomers of approximately 150 amino acids each, which exhibit

exclusive specificity towards mannose. Lectins from Moraceae (jacalin, MPA, artocarpin), Convulvulaceae (calsepa, conarva), Asteraceae (heltuba), Gramineae (barley and wheat lectins) and Musaceae (banana lectin) together constitute the Jacalin lectin family (Bourne *et al.*, 1999). They occur in seeds as well as in vegetative tissues. Jacalins exhibit low sequence similarity and differ with respect to their carbohydrate binding specificity.

Type2 RIPs (Ribosome Inactivating Proteins) Lectins with ricin-B domains :

This group of plant lectins were previously referred to as the family of ribosome-inactivating proteins (RIPs), due to the fact that these proteins were first identified as plant proteins that inactivate eukaryotic ribosomes through the removal of a conserved adenine residue from the ribosomal RNA (Van Damme *et al.*, 2001 and Stirpe, 2004). Based on their molecular structure RIPs are subdivided into type-1, type-2 and type-3 RIPs. The B-chain of type-2 RIPs classified as lectin domain and this lectin domain is referred to as the ricin-B-domain, named after 'ricin' the first RIP isolated from seeds of *Ricinus communis* (Lord *et al.*, 1994).

Amaranthins:

The Amaranthus family, which is called after the *Amaranthus caudatus* seed lectin is a rather small family of closely related lectins found in different Amaranthus species. All known amaranthins are homodimers built of 33kDa subunits. Detailed specificity studies have shown that amaranthins preferentially recognizes the T-antigen disaccharide Gal β and GalNAc (Rinderle *et al.*, 1989). This protein is a homodimer having a ' β -trefoil fold', just like type2 RIPs. It has no sequence homology with B chain of the latter one. Its carbohydrate binding site is also different from that of RIPs. Amaranthin subunit folds into two β -trefoil domains; one of them is involved in carbohydrate binding and the other in oligomerisation (Transue *et al.*, 1997)

Cucurbitaceae phloem lectins:

The family of cucurbitaceae phloem lectins is a small group of chitin binding agglutinin found in the phloem exudates of a number of cucurbitaceae species (Sabnis and Hart, 1978). These lectins, also called phloem proteins PP2, are dimeric proteins built up of subunits of approximately 22kDa. Cucurbitaceae phloem lectins are

found only in the phloem exudates of many cucurbitaceae. These lectins are specific for oligomers of GlcNAc (Wang *et al.*, 1994). These lectins have high sequence similarity and found in some species of *Trichosanthes*, *Telfaira* and *Mamordica*. Seeds of serpent cucumber (*Trichosanthes kirilowii*) contain a glycosylated galactose specific lectin composed of disulfide-linked subunits of 37 kDa and 25 kDa (Falasca *et al.*, 1989). Similar seed lectins from *Trichosanthes anguina* (snake gourd) (Komath and Swamy, 1998) and *Trichosanthes cucumerina* species (Padma *et al.*, 1999) have been isolated and characterized. Another seed lectin from fluted gourd (*Telfaira occidentalis*) is a hexameric protein with three pairs of disulphide-linked subunits of 30 kDa (Peumans and Van Damme, 1999). A galactose specific seed lectin from *Mamordica charanita* species has also been characterized (Das *et al.*, 1981). No three-dimensional structure is yet available for this family. However, recent preliminary X-ray studies of lectins from serpent cucumber (Li *et al.*, 2000) and snake gourd (Manoj *et al.*, 2001) indicate structural homology with type2 RIPs.

Lectin-Carbohydrate specificity and interactions:

Although lectins were discovered some 100 years ago, their involvement in carbohydrate recognition has been seriously dealt with only in the past two decades (Hughes, 1992; Lis and Sharon, 1998; Sharon and Lis, 1989 and 1990). Now it is well known that all cells carry carbohydrates on their surface in the form of glycoconjugates (Cook *et al.*, 1986) and lectins mediate cell-cell recognition by binding surface carbohydrates (Lis and Sharon, 1998). These surface carbohydrates on a cell serve as points of attachment for other cells, and pathogens. Sharon and Lis (1989) have proposed that the lectin mediated cell-cell interaction takes place through mechanisms like: 1) Cell surface lectins binding to soluble glycoproteins can create inter cell bridges. 2) Lectins can bind carbohydrates of insoluble components of the extra cellular matrix that promote cell adhesion. 3) Soluble lectins binding to carbohydrates on a pair of opposing cells can act as bridge for these two cells.

The atomic basis of lectin-carbohydrate interactions has been elucidated through X-ray crystallographic analysis of a variety of lectin-carbohydrate complexes. The forces, which hold the lectin-carbohydrate complexes together are, hydrogen bond networks, metal

coordination, van der Waals and hydrophobic interactions (Drickamer, 1995; Elgavish and Shannan, 1997). Lectins apply various strategies to generate carbohydrate specificity, evident from crystal structures of lectin-sugar complexes. They are: 1) The variation in quaternary structure generates carbohydrate specificity in the case of legume lectins and bulb lectins (Chandra *et al.*, 1999; Vijayan and Chandra, 1999). In both cases, the small alterations in essentially same tertiary structure lead to different quaternary structures that discriminate between different sugar ligands, 2) Post-translational modification generating carbohydrate specificity has been observed in the structures of jacalin (Sankaranarayanan *et al.*, 1996) and related lectins (Vijayan and Chandra, 1999), 3) Water molecules generating sugar specificity is seen in sugar complexes of PNA, Ecor1 and other lectins (Elgavish and Shannan, 1998; Ravishankar *et al.*, 1997), 4) Through their extended binding sites (subsite) and subunit multivalency.

Plant lectins: from edible sources:

Lectins are present in the most commonly edible plant foods such as avocado, beans, beetroot, blackberries, cabbage, carrots, cherries, corn, garlic, leek, mushrooms, nuts, oregano, parsley, peanuts, peas, potato, rice, soybeans, spices, tea, tomato, wheat germ and also in several non-cultivated plant species (Nachbar and Oppenheim, 1980; Liener *et al.*, 1986; Gupta and Sandhu, 1998; Oliveira *et al.*, 2000 and Leontowicz *et al.*, 2001), the exposure of heterotroph organisms, including human beings, to functionally active lectins is a common event. Actually, the presence of nutritionally significant amounts of active lectins in fresh and processed foods and the lack of public knowledge concerning the deleterious effects of dietary lectins on the gut and health have led to a number of outbreaks of food poisoning.

Lectins: resistance to proteolysis:

Many plant lectins in particular have been found to be resistant to degradation by proteases *in vitro* (Carbonaro *et al.*, 1997) and in the gut *in vivo* (Pusztai, 1991). PHA (Pusztai *et al.*, 1979 and Hara *et al.*, 1984), ConA (Nakata and Kimura, 1985), ConBr (*Canavalia brasiliensis*) (Oliveira *et al.*, 1994), PTA (*Psophocarpus tetragonolobus*; winged bean) (Higuchi *et al.*, 1983), LEA (*Lycopersicon esculentum*; tomato) (Kilpatrick *et al.*, 1985), GNA, SBA, WGA, PSA, SNA-

I, SNA-II (*Sambucus nigra*; elderberry), VFL (*Vicia faba*; broad bean) and DGL (*Dioclea grandiflora*; mucuna) (Pusztai, 1991 and Bardocz *et al.*, 1995) were all showed to be resistant to *in vivo* breakdown by proteolytic enzymes. It is also noteworthy that far less of the lectins survive the *in vitro* treatment with proteolytic enzymes (Rios *et al.*, 1996). This was the case for ConBr, CAA and DGL, all glucose-mannose specific lectins, which were digested to a far higher extent (52–84%) than *in vivo*. Thus, it is possible that in the gut the lectins may even be protected from proteolytic degradation during gut passage perhaps as a result of binding to epithelial or luminal gut components. The slight protection from proteolytic degradation *in vitro* conveyed by adding glucose, Ca⁺² and Mn⁺² to the reaction mixture is consistent with this possibility. Nevertheless, as a result of high resistance to proteolytic degradation *in vivo* nutritionally significant amounts of certain dietary lectins will survive in an intact and highly reactive form within the gut lumen.

Lectins: their effects on the digestive tract :

As most lectins are not degraded during their passage through the digestive tract they are able to bind the epithelial cells which express carbohydrate moieties recognized by them. This event is undoubtedly the second one in importance for determining the toxicity of orally fed lectins. Indeed, lectins which are not bound by the mucosa usually induce little or no harmful anti-nutritive effect for the consumers (Pusztai and Bardocz, 1996). Once bound to the digestive tract, the lectin can cause dramatic changes in the cellular morphology and metabolism of the stomach and/ or small intestine and activate a cascade of signals which alters the intermediary metabolism. Thus, lectins may induce changes in some, or all, of the digestive, absorptive, protective or secretory functions of the whole digestive system and affect cellular proliferation and turnover.

Lectin: mechanism of toxicity and their insecticidal properties:

The insecticidal activity of plant lectins against a large array of insect species belonging to the orders coleoptera, homoptera, diptera and lepidoptera have been well documented (Gatehouse *et al.*, 1995; Schuler *et al.*, 1998 and Carlini and Grossi-de-Sa, 2002). Although the precise mode of insecticidal action of plant lectins is

not fully understood it appears that resistance to proteolytic degradation by the insect digestive enzymes and binding to insect gut structures are two basic prerequisites for lectins to exert their deleterious effects on insects. After binding to the surface of the intestinal epithelial cells, lectins will interfere with the digestive, protective or secretory functions of the intestine. Binding of a lectin to a receptor might decrease the absorption of nutrients and/or disrupt the midgut epithelial cells (Gatehouse *et al.*, 1984 and Eisemann *et al.*, 1994). Immunological studies carried out to elucidate the mechanism of action of the mannose-specific lectins GNA on the rice brown planthoppers, showed that no proteolytic degradation occurred either in the gut or honeydew of insects which fed on lectin containing diet (Powell *et al.*, 1998). It was shown by Zhu-Salzman *et al.* (1996) that there is a correlation between receptor binding and toxicity of the lectin isolated from leaves of *Griffonia simplicifolia* towards the cowpea bruchid beetle (*Callosobruchus maculatus*). Similar results were reported against *Lipaphis erysimi* and *Aphis craccivora* using lectin isolated from edible *Arum maculatum* tubers (Majumder *et al.*, 2004). In addition, Du *et al.* (2000) reported that ferritin acts as the most abundant binding protein for GNA in the midgut of BPH (*Nilaparvata lugens*). The resistance to proteolytic degradation and binding of ASAL to gut receptors in the luminal epithelium of two important insect pests, the mustard aphid (*Lyphaphis erysimi*) and the red cotton bug (*Dysdercus cingulatus*) have been well documented (Bandyopadhyay *et al.*, 2001).

A wide range of lectins exhibiting either mannose or mannose/glucose sugar binding affinity, including *Gallanthus nivalis* agglutinin (GNA), Concanavalin A (Con A) and *Pisum sativum* agglutinin (PSA), *Allium sativum* agglutinin (ASA) revealed palpable antimetabolic effects towards members of the homopteran insects both under *in vitro* (Habibi *et al.*, 1993; Powell *et al.*, 1993 and Rahbe *et al.*, 1995) as well as *in planta* conditions (Powell *et al.*, 1993, 1995a and Gatehouse *et al.*, 1996). Amongst mannose-binding lectin genes, *Gallanthus nivalis* agglutinin (*gna*) gene has been introduced and expressed in diverse crop plants, viz., rice (Rao *et al.*, 1998; Foissac *et al.*, 2000; Tinjuangjun *et al.*, 2000; Fitches *et al.*, 2001; Maqbool *et al.*, 2001; Tang *et al.*, 2001; Wu *et al.*, 2002; Nagadhara *et al.*, 2003, 2004), wheat (Stoger *et al.*, 1999), tobacco (Hilder *et al.*, 1995)

and potato (Down *et al.*, 1996; Sauvion *et al.*, 1996; Gatehouse *et al.*, 1996, 1997; Bell *et al.*, 2001; Couty *et al.*, 2001) against different pests. Similarly, *Allium sativum* mannose-specific lectin (*asa* and *asal*) genes have been introduced into rice (Saha *et al.*, 2006 and Yarasi *et al.*, 2008) and tobacco plants (Bandyopadhyay *et al.*, 2001 and Sadeghi *et al.*, 2007); which exhibited ample resistance against homopteran and lepidopteran pests.

ASAL transgenics and their insecticidal activity :

It has been shown that the most of the characteristic odour of the *Allium* species including vegetables onion and garlic is due to the enzymatic degradation of sulfur-containing amino acids (Fowden, 1964). The enzyme involved in this process is allinase which is known to represent an important fraction of the total protein content in *Allium* bulbs and leaves. Since then there has been numerous reports on the occurrence, purification and characterization of allinases from several Alliaceae species were published (Tobkin and Mazelis, 1979; Nock and Mazelis, 1986, 1987 and Fugita *et al.*, 1990). The isolation and characterization of mannose-specific lectin from *A. sativum* (garlic), a representative of the plant family Alliaceae was done by Van Damme *et al.* (1991). In contrast to Amaryllidaceae lectins which are composed of identical 12 kDa subunits the garlic lectins apparently consist of two different sub units of 11.5 kDa and 12.5 kDa referred to as ASAI (heterodimer) and 12 kDa subunit in ASAI (homodimer). Transgenic plants expressing ASA and ASAI showed a reduction in *S. littoralis* larval weight when fed in an artificial diet (Fitches *et al.*, 1997). Since ASA and ASAI adversely affected the weight gain in the larval stages, the development into pupae was retarded. Bandyopadhyay *et al.* (2001) documented that ASAL binds to the carbohydrate part of the 55 and 45 kDa brush border membrane vesicle receptor proteins in mustard aphid (*Lymphaphis erysimi*) and red cotton bug (*Dysdercus cingulatus*), respectively. It was suggested that binding of ASAL to these receptors may decrease the permeability of the membrane. Earlier studies demonstrated that the garlic bulb lectin ASA, exhibited a significant antimetabolic effects towards third instar nymphs of the rice brown planthopper (BPH) when fed on an artificial diet (Powell *et al.*, 1995b). Roy *et al.* (2002) showed that ASA exhibited high mortality upto

78% against the red cotton bug (*Dysdercus cingulatus*) when added to an artificial diet. The ASAL transgenic tobacco plants exhibited insecticidal activity against mustard aphid (Dutta *et al.*, 2005a) and also reduced the survival and fecundity capacity of the peach potato aphid (Dutta *et al.*, 2005b). The insecticidal activity of the ASAL and ASAI in transgenic tobacco plants against tobacco aphid (*Myzus nicotianae*) was reported by Sadeghi *et al.* (2007). Transgenic cotton expressing ASAI and ASAL exerted a significant detrimental effect on larval development, growth and survival of the major lepidopteran pest *Spodoptera littoralis* (Sadeghi *et al.*, 2008). Transgenic rice expressing ASAL exhibited ample resistance against homopteran insects BPH and GLH (Saha *et al.*, 2006) and for BPH, GLH and WBPH (Yarasi *et al.*, 2008).

Conclusion :

It has been extensively demonstrated that plant lectins are effective biological agents against insect attack. In fact, insect resistant transgenic plants produced by expression of lectin genes are already a reality. This approach could increase crop productivity and reduce the usage of pesticide. However, few lectins tested for this purpose have been specifically selected on the basis that they convey high resistance to predators of plants.

REFERENCES

- Bandyopadhyay, S.,** Roy, A. and Das, S. (2001). Binding of garlic (*Allium sativum*) leaf lectin to the gut receptors of homopteran pests is correlated to its insecticidal activity. *Plant Sci.*, **161**: 1025-1033.
- Bardocz, S.,** Ewen, S.W.B., Grant, G. and Pusztai, A. (1995). Lectins as growth factors of the small intestine and the gut. In: Pusztai, A., Bardocz, S. (Eds.), *Lectins: Biomedical Perspectives*, Taylor and Francis, London, pp. 103–116.
- Barre, A.,** Van Damme, E.J.M., Peumans, W.J. and Rouge, P. (1996). Structure function relationship of monocot mannose-binding lectins. *Plant Physiol.*, **112** : 1531-1540.
- Bell, H.A.,** Fitches, E.C., Down, R.E., Ford, L., Marris, G.C., Edwards, J.P., Gatehouse, J.A. and Gatehouse, A.M.R. (2001). Effect of dietary cowpea trypsin inhibitor (CpTI) on the growth and development of the tomato moth *Lacanobia oleracea* (Lepidoptera: Noctuidae) and on the success of the gregarious ectoparasitoid *Eulophus pennicornis* (Hymenoptera: Eulophidae). *Pest Manage Sci.*, **57** : 57-65.
- Bourne, Y.,** Zamboni, V., Barre, A., Peumans, W.J., Van Damme,

- E. J. M. and Rouge, P. (1999). Helianthus tuberosus lectin reveals a widespread scaffold for mannose-binding lectins. *Structure*, **7**: 1473-1482.
- Boyd, W.C.** and Slapeigh, E. (1954). Specific precipitating activity of plant agglutinins (lectins). *Sci.*, **119**: 419.
- Carbonaro, M.**, Cappelloni, M., Nicoli, S., Lucarini, M. and Carnovale, E. (1997). Solubility-digestibility relationship of legume proteins. *J. Agric. Food Chem.*, **45**: 3387-3394.
- Carlini, C.R.** and Grossi-de-Sa, M.F. (2002). Plant toxic proteins with insecticidal properties. A review on their potentialities as bioinsecticides. *Toxicon.*, **20**: 1515-1539.
- Chandra, N.R.**, Ramachandraiah, G., Bachawat, Dam, T.K., Surolia, A. and Vijayan, M. (1999). Crystal structure of a dimeric mannose-specific agglutinin from garlic: Quaternary association and carbohydrate specificity. *J. Mol. Biol.*, **285**: 1157-1168.
- Cook, G.M.W.** (1986). Cell surface carbohydrates: molecules in search of a function? *J. Cell. Sci.*, **4**: 45-70.
- Couty, A.**, Down, R.E., Gatehouse, A.M.R., Kaiser, L., Pham-Delegue, M.H. and Poppy, G.M. (2001). Effects of artificial diet containing GNA and GNA expressing potatoes on the development of the aphid parasitoid *Aphidius ervi* Haliday (Hymenoptera: Aphididae). *J. Insect Physiol.*, **47**: 1357-1366.
- Das, M.K.**, Khan, M.I. and Surolia, A. (1981). Fluorimetric studies of the binding of Momordica charantia lectin with ligands. *Biochem. J.*, **195**: 341-343.
- Down, R.E.**, Gatehouse, A.M.R., Hamilton, W.D.O. and Gatehouse, J.A. (1996). Snowdrop lectin inhibits development and decreases fecundity of the glasshouse potato aphid (*Aulacorthum solani*) when administered in vitro and via transgenic plants both in laboratory and glasshouse trials. *J. Insect Physiol.*, **42**: 1035-1045.
- Drickamer, K.** (1995). Multiplicity of lectin-carbohydrate interactions. *Nat. Struct. Biol.*, **2**: 437-439.
- Du, J.**, Foissac, X., Carss, A., Gatehouse, A.M.R. and Gatehouse, J.A. (2000). Ferritin acts as the most abundant binding protein for snowdrop lectin in the midgut of rice brown planthoppers (*Nilaparvata lugens*). *Insect Biochem. & Mol. Biol.*, **30**: 297-305.
- Dutta, I.**, Majumder, P., Saha, P., Sakar, A., Ray, K. and Das, S. (2005a). Constitutive and phloem specific expression of *Allium sativum* leaf agglutinin (ASAL) to engineer aphid (*Lipaphis erysimi*) resistance in transgenic Indian mustard (*Brassica juncea*). *Plant Sci.*, **169**: 996-1007.
- Dutta, I.**, Saha, P., Majumder, P., Sakar, A., Chakraborti, D., Banerjee, S. and Das, S. (2005b). The efficacy of novel insecticidal protein, *Allium sativum* leaf lectin (ASAL), against homopteran insects monitored in transgenic tobacco. *Plant Biotechnol. J.*, **3**: 601-611.
- Eisemann, C.H.**, Donaldson, R.A., Pearson, R.D., Cadagon, L.C., Vuocolo, T. and Pellam, R.L. (1994). Larvicidal action of lectins on *Lucilia cuprina*; mechanism of action. *Entomol. Exp. Appl.*, **72**: 1-11.
- Elgavish, S.** and Sahnann, B. (1997). Lectin-Carbohydrate interactions: different folds, common recognition principles. *Trends Biochem. Sci.*, **22**: 462-467.
- Elgavish, S.** and Sahnann, B. (1998). Structure of Erythrina corallodendron lectin and of its complexes with mono and disaccharides. *J. Mol. Biol.*, **277**: 917-932.
- Falasca, A.I.**, Abbondanza, A., Barbieri, L., Bolognesi, A., Rossi, C.A. and Stirpe, F. (1989). Purification and partial characterization of a lectin from the seeds of *Trichosanthes kirilowii* Maximowicz. *FEBS Letters*, **246**: 159-62.
- Fitches, E.**, Gatehouse, A.M.R. and Gatehouse, J.A. (1997). Effects of snowdrop lectin (GNA) delivered via artificial diet and transgenic plants on the development of tomato moth (*Lacanobia oleracea*) larvae in laboratory and glasshouse trials. *J. Insect. Physiol.*, **43**: 727-739.
- Fitches, E.**, Woodhouse, S.D., Edwards, J.P. and Gatehouse, J.A. (2001). *In vitro* and *in vivo* binding of snowdrop lectin (*Galanthus nivalis* agglutinin; GNA) and jackbean (*Canavalia ensiformis*; Con A) lectins within tomato moth (*Lacanobia oleracea*) larvae; mechanism of insecticidal action. *J. Insect. Physiol.*, **47**: 777-787.
- Foissac, X.**, Loc, N.T., Christou, P., Gatehouse, A.M.R. and Gatehouse, J.A. (2000). Resistance to green leafhopper (*Nephotettix virescens*) and brown planthopper (*Nilaparvata lugens*) in transgenic rice expressing snowdrop lectin (*Galanthus nivalis* agglutinin; GNA). *J. Insect Physiol.*, **46**: 573-583.
- Fowden, L.** (1964). The chemistry and metabolism of recently isolated amino acids. *Annu. Rev. Biochem.*, **33**: 173-204.
- Fujita, M.**, Endo, M. and Sano, M. (1990). Purification and characterization of Allin lyase from welsh onion (*Allium fistulosum*). *Agric. Biol. Chem.*, **54**: 1077-1079.
- Gatehouse, A.M.R.**, Dewey, F.M., Dove, J., Fenton, K.A. and Pusztai, A. (1984). Effect of seed lectin from *Phaseolus vulgaris* on the development of larvae of *Callosobruchus maculatus*; mechanism of toxicity. *J. Sci. Food Agri.*, **35**: 373-380.
- Gatehouse, A.M.R.**, Davison, G.M., Newell, C.A., Merryweather, A., Hamilton, W.D.O., Burgess, E.P.J., Gilbert, R.J.C. and Gatehouse, J.A. (1997). Transgenic potato plants with enhanced resistance to the tomato moth (*Lacanobia oleraceae*) growth room trials. *Mol. Breed.*, **3**: 49-63.

- Gatehouse, A.M.R.**, Powell, K.S., Peumans, W.J., Van Damme, E.J.M. and Gatehouse, J.A. (1995). Insecticidal properties of plant lectins: their potential in plant protection. In: Lectins: Biomedical Perspectives (Pustzai A and Bardocz S eds). London: Taylor and Francis. pp, 35-58.
- Gatehouse, A.M.R.**, Down, R.E., Powell, K.S., Sauvion, N., Rahbe, Y., Newell, C.A., Merryweather, A., Hamilton, W.D.O. and Gatehouse, J.A. (1996). Transgenic potato plants with enhanced resistance to peach-potato aphid *Myzus persicae*. *Entomol. Exp. Appl.*, **79** : 295-307.
- Gupta, A.** and Sandhu, R.S. (1998). Effect of garlic agglutinin and garlic extracts on the rat jejunum. *Nutr. Res.*, **18** : 841-850.
- Habibi, J.**, Backus, E.A. and Czaplá, T.H. (1993). Plant lectins affect survival of the potato leafhopper (Homoptera: Cicadellidae). *J. Econ. Entomol.*, **86** : 945-951.
- Higuchi, M.**, Suga, M., Iwai, K. (1983). Participation of lectin in biological effects of raw winged bean seeds on rats. *Agric. Biol. Chem.*, **47** : 1979-1986.
- Hilder, V.A.**, Powell, K.S., Gatehouse, A.M.R., Gatehouse, J.A., Gatehouse, L.N., Shi, Y., Hamilton, W.D.O., Merryweather, A., Newell, C.A., Timans, J.C., Peumans, W.J., Vandamme, E.J.M. and Boulter, D. (1995). Expression of snowdrop lectin in transgenic tobacco plants results in added protection against aphids. *Trans. Res.*, **4** : 18-25.
- Hughes, R.C.** (1992). Lectins as cell adhesion molecules. *Curr. Opin. Struct. Biol.*, **2** : 687-692.
- Kilpatrick, D.C.**, Pusztai, A., Grant, G., Graham, C. and Ewen, S.W.B. (1985). Tomato lectin resists digestion in the mammalian alimentary canal and binds to intestinal villi without deleterious effects. *FEBS Lett.*, **185** : 299-305.
- Komath, S.S.** and Swamy, M.J. (1998). Further characterization of snake gourd (*Trichosanthes anguina*) seed lectin. *Curr. Sci.*, **75** : 608-611.
- Leontowicz, H.**, Leontowicz, M., Kostyra, H., Kulasek, G., Gralak, M.A., Krzeminski, R. and Podgurniak, M. (2001). Effects of raw or extruded legume seeds on some functional and morphological gut parameters in rats. *J. Anim. Feed Sci.*, **10** : 169-183.
- Li, M.**, Wang, P.Y., Chai, J.J., Wang, Y.K. and Bi, C. (2000). Molecular-replacement studies of *Trichosanthes kirilowii* lectin 1: a structure belonging to the family of type2 ribosome-inactivating proteins. *Acta Crystgr.*, **D56** : 1073-1075.
- Liener, I.**, Young, M. and Lovrien, R. (1986). Lectins inhibit digestive enzymes and so survive alimentary passage. *FASEB J.*, **45** : 1573-1573.
- Lis, H.** and Sharon, N. (1998). Lectins: Carbohydrate-specific proteins that mediate cellular recognition. *Chem. Rev.*, **98** : 637-674.
- Lord, J.M.**, Roberts, L.M. and Robertus, J.D. (1994). Ricin: Structure, mode of action, and some current applications. *FASEB. J.*, **8** : 201-208.
- Majumder, P.**, Banerjee, S. and Das, S. (2004). Identification of receptors responsible for binding of the mannose specific lectin to the gut epithelial membrane of the target insects. *Glycoconj J.*, **20** : 525-530.
- Manoj, N.**, Jayprakash, A.A., Pratap, J.V., Komath, S.S., Swamy, M.J. and Vijayan, M. (2001). Crystallization and preliminary X-ray studies of snake gourd lectin: homology with type II ribosome-inactivating proteins. *Acta Crystallogr.*, **D57** : 912-914.
- Maqbool, S.B.**, Riazuddin, S., Loc, N.T., Gatehouse, A.M.R., Gatehouse, J.A. and Christou, P. (2001). Expression of multiple insecticidal genes confers broad resistance against a range of different rice pests. *Mol Breed.*, **7** : 85-93.
- Nachbar, M.S.** and Oppenheim, J.D. (1980). Lectins in the United States diet: a survey of lectins in commonly consumed foods and a review of the literature. *Am. J. Clin. Nutr.*, **33** : 2338-2345.
- Nagadhara, D.**, Ramesh, S., Pasalu, I.C., Rao, Y.K., Krishnaiah, N.V., Sarma, N.P., Bown, D.P., Gatehouse, J.A., Reddy, V.D. and Rao, K.V. (2003). Transgenic indica rice resistant to sap sucking insects. *Plant Biotechnol J.*, **1** : 231-240.
- Nagadhara, D.**, Ramesh, S., Pasalu, I.C., Rao, Y.K., Sarma, N.P., Reddy, V.D. and Rao, K.V. (2004). Transgenic rice plants expressing the snowdrop lectin gene (*gna*) exhibit high-level resistance to the whitebacked planthopper (*Sogatella furcifera*). *Theor. Appl. Genet.*, **109** : 1399-1405.
- Nakata, S.** and Kimura, T. (1985). Effect of ingested toxic bean lectins on the gastrointestinal tract in the rat. *J. Nutr.*, **115** : 1621-1629.
- Nock, L.P.** and Mazelis, M. (1986). The carbon-sulfur lyases of higher plants: preparation and properties of homogeneous alliin lyase from garlic (*Allium sativum*). *Arc Biochem Biophys.*, **249** (1): 27-33.
- Nock, L.P.** and Mazelis, M. (1987). The C-S lyases of higher plants: Direct comparison of the physical properties of homogeneous alliin lyase of garlic (*Allium sativum*) and onion (*Allium cepa*). *Plant Physiol.*, **85** (4): 1079-1083.
- Oliveira, J.T.A.**, Vasconcelos, I.M., Bezerra, L.C.N.M., Silveira, S.B., Monteiro, A.C.O. and Moreira, R.A. (2000). Composition and nutritional properties of seeds from *Pachira aquatica* Aubl, *Sterculia striata* St Hil et Naud and *Terminalia catappa* Linn., Food Chem. 70, 185-191.
- Oliveira, J.T.A.**, Vasconcelos, I.M., Gondim, M.J.L., Cavada, B.S., Moreira, R.A., Santos, C.F. and Moreira, L.I.M. (1994).

- Canavalia brasiliensis seeds. Protein quality and nutritional implications of dietary lectin. *J. Sci. Food Agric.*, **64** : 417–424.
- Padma, P.**, Komath, S.S., Nadimpalli, S.K. and Swamy, M.J., (1999). Purification in high yield and characterization of a new galactose-specific lectin from the seeds of *Trichosanthes cucumerina*. *Phytochemistry*, **50** : 363-371.
- Peumans, W.J.**, Verhaert, P., Pfuller, U. and Van damme, E.J.M. (1996). Isolation and characterization of a small chitin binding lectin from mistletoe (*Viscum album*). *FEBS. Letters*, **396** : 261-265.
- Peumans, W.J.** and Van Damme, E.J.M. (1999). Seed lectins., In; Seed proteins., Shewry, P.R. and Casey, R., eds., Kluwer Academic Publishers, The Netherlands, 657-683.
- Powell, K.S.**, Gatehouse, A.M.R., Hilder, V.A. and Gatehouse, I.A. (1993). Antimetabolic effects of plant lectins and plant and fungal enzymes on the nymphal stages of 2 important rice pests, *Nilaparvata lugens* and *Nephotettix virescens*. *Entomol. Exp. Appl.*, **66** : 119-126.
- Powell, K.S.**, Gatehouse, A.M.R., Hilder, V.A. and Gatehouse, J.A. (1995). Antifeedant effects of plant lectins and an enzyme on the adult stage of rice brown planthopper, *Nilaparvata lugens*. *Entomol. Exp. Appl.*, **75** : 51-59.
- Powell, K.S.**, Spence, J., Bharathi, M., Gatehouse, J.A. and Gatehouse, A.M.R. (1998). Immunohistochemical and developmental studies to elucidate the mechanism of action of the snowdrop lectin on the rice brown planthopper *Nilaparvata lugens* (Stal). *J. Insect Physiol.*, **44** : 529-539.
- Pusztai, A.** (1991). General effects on animal cells. In: Pusztai, A., (Ed.), *Plant Lectins*, Cambridge University Press, Cambridge, pp. 105–205.
- Pusztai, A.**, Clarke, E.M.W. and King, T.P. (1979). The nutritional toxicity of *Phaseolus vulgaris* lectins. *Proc. Nutr. Soc.*, **38** : 115–120.
- Pusztai, A.** and Bardocz, S. (1996). Biological effects of plant lectins on the gastrointestinal tract: metabolic consequences and applications. *Trends Glycosci. Glys.*, **8** : 149–165.
- Rahbe, Y.**, Sauvion, N., Febvay, G., Peumans, W.J. and Gatehouse, A.M.R. (1995). Toxicity of lectins and processing of ingested proteins in the pea aphid *Acyrtosiphon pisum*. *Entomol. Exp. Appl.*, **76** : 143-155.
- Raikhel, N.V.**, Lee, H. I. and Borekaert, W.F. (1993). Structure and function of chitinbinding proteins. *Ann. Rev. Plant Physiol. & Plant Mol. Biol.*, **44** : 591-615.
- Rao, K.V.**, Rathore, K.S., Hodges, T.K., Fu, X., Stoger, E., Sudhakar, D., Williams S., Christou P., Bharathi M., Bown, D.P., Powell, K.S., Spence, J., Gatehouse, A.M.R. and Gatehouse, J.A. (1998). Expression of snowdrop lectin (GNA) in transgenic rice plants confers resistance to rice brown planthopper. *Plant J.*, **15** : 469-477.
- Ravishankar, R.**, Ravindran, M., Suguna, K., Surolia, A. and Vijayan, M. (1997). Crystal structure of peanut lectin-T-antigen complex: carbohydrate specificity generated by water bridges. *Curr. Sci.*, **72** : 855-861.
- Rios, F.J.B.**, Cavada, B.S., Medeiros, D.A., Moreira, R.A., Vasconcelos, I.M. and Oliveira, J.T.A. (1996). Digestibility of plant lectins from *Canavalia*, *Cratylia*, *Dioclea* and *Artocarpus* Genera. In: Van Driessche, E., Rouge´, P., Beeckmans, S., Bog-Hansen, T.C. (Eds.), *Lectins: Biology, Biochemistry, Clinical Biochemistry*, Textop, Denmark, pp. 277–284.
- Rouge, P.**, Cambillu, C. and Bourne, Y. (1991). The three-dimensional structure of legume lectins. In: *Lectin Reviews.*, Kilpatrick, D. C., Van Driessche, E. and Bog-Hansen, T. C. eds., Vol.1, Sigma Chemical co., St.Louis, USA, pp.143-159.
- Roy, A.**, Banerjee, S., Majumder, P. and Das, S. (2002). Efficiency of mannose binding plant lectins in controlling a homopteran insect, the red cotton bug. *J. Agric. Food Chem.*, **50** : 6775-6779.
- Sadeghi, A.**, Broeders, S., Hernalsteens, J.P., De Greve, H., Peumans, W.J., Van Damme, E.J.M. and Smagghe, G. (2007). Expression of garlic leaf lectin under the control of the phloem-specific promoter *Asu1* from *Arabidopsis thaliana* protects tobacco plants against the tobacco aphid (*Myzus nicotianae*). *Pest Manage Sci.*, **63**: 1215-1223.
- Sadeghi, A.**, Smagghe, G., Broeders, S., Hernalsteens, J.P., De Greve, H., Peumans, W.J. and Van Damme, E.J.M. (2008). Ectopically expressed leaf and bulb lectins from garlic (*Allium sativum* L.) protect transgenic tobacco plants against cotton leaf worm (*Spodoptera littoralis*). *Trans Res.*, **17**: 9-18.
- Saha, P.**, Majumder, P., Dutta, I., Ray, T., Roy, S.C. and Das, S. (2006). Transgenic rice expressing *Allium sativum* leaf lectin with enhanced resistance against sap-sucking insect pests. *Planta.*, **223**: 1329-1343.
- Sauvion, N.**, Rahbe, Y., Peumans, W.J., Van Damme, E.J.M., Gatehouse, J.A. and Gatehouse, A.M.R. (1996). Effects of GNA and other mannose binding lectins on development and fecundity of the peach-potato aphid *Myzus persicae*. *Entomol. Exp. Appl.*, **79** : 285-293.
- Schuler, T.H.**, Poppy, G.M., Kerry, B.R. and Denholm, I. (1998). Insect resistant transgenic plants. *Trends Biotechnol.*, **16**: 168-174.
- Sharon, N.** and Lis, H. (1989). Lectins as cell recognition molecules. *Sci.*, **246** : 227-234.
- Sharon, N.** and Lis, H. (1990). Legume lectins –a large family of homologous proteins. *The FASEB. J.*, **4** : 3198-3208.

- Sharon, N.** and Lis, H. (1993). Carbohydrates in cell recognition. *Scientific American*, 74-80.
- Smith, J.J.** and Raikhel, N.V. (1989). Nucleotide sequences of cDNA clone encoding wheat germ agglutinin isolectins A and D. *Plant Mol. Biol.*, **13** : 601-603.
- Stillmark, H.** (1888). Uber Ricin ein giftiges Ferment aus den Samen von Ricinus communis. L. und einige anderen Euphorbiaceen. Inagural Disseration Dorpat.
- Stoger, E.,** Williams, S., Christan, P., Down, R.E. and Gatehouse, J.A. (1999). Expression of the insecticidal lectin from snowdrop (*Galanthus nivalis* agglutinin; GNA) in transgenic wheat plants: effects on predation by the grain aphid *Sitobion avenae*. *Mol. Breed.*, **5** : 65-73.
- Tang, J.D.,** Collins, H.L., Metz, T.D., Earle, E.D., Zhao, J.Z., Roush, R.T. and Shelton, A.M. (2001). Greenhouse tests on resistance management of Bt transgenic plants using refuge strategies. *J. Econ. Entomol.*, **94** : 240-247.
- Tinjuangjun, P.,** Loc, N.T., Gatehouse, A.M.R., Gatehouse, J.A. and Christou, P. (2000). Enhanced insect resistance in Thai rice varieties generated by particle bombardment. *Mol. Breed.*, **6** : 391-399.
- Tobkin, H.E.Jr.** and Mazelis, M. (1979). Alliin lyase: preparation and characterization of the homogeneous enzyme from onion bulbs. *Arch. Biochem. Biophys.*, **193**: 150-157.
- Van Damme, E.J.M.,** Allen, A.K. and Peumans, W.J. (1987). Isolation characterization of a lectin with exclusive specificity towards mannose snowdrop (*Galanthus nivalis*) bulbs. *FEBS Letters*, **215** : 140-144.
- Van Damme, E.J.M.,** Goldstein, I.J. and Peumans, W.J. (1991). A comparative study of related mannose-binding lectins from the Amaryllidaceae and Alliaceae. *Phytochem.*, **30** : 509-514.
- Van Damme, E.J.M.,** Peumans, W.J., Barre, A. and Rouge, P. (1998). Plant lectins: a composite of several distinct families of structurally and evolutionarily related proteins with diverse biological roles. *Crit. Rev. Plant. Sci.*, **17** : 575-692.
- Van Damme, E.J.M.,** Hao, Q., Chen, Y., Barre, A., Vandenbussche, F., Desmyter, S., Rouge, P. and Peumans, W.J. (2001). Ribosome-inactivating proteins: a family of plant proteins that do more than inactivate ribosomes. *Crit. Rev. Plant Sci.*, **20** : 395-465.
- Vijayan, M.** and Chandra, N. (1999). Lectins. *Curr. Opin. Stru. Biol.*, **9** : 707-714.
- Wang, M.B.,** Boulter, D. and Gatehouse, J. (1994). Characterization and sequencing of cDNA clone encoding for phloem protein PP2 of *Cucurbita pepo*. *Plant Mol. Biol.*, **24** : 159-170.
- Wu, D.X.,** Shu, Q.Y., Wang, Z.H., Cui, H.R. and Xia, Y.W. (2002). Quality variations in transgenic rice with a synthetic cry1Ab gene from *Bacillus thuringiensis*. *Plant Breed.*, **121**: 198-202.
- Yarasi, B.,** Vijaya, K.S., Pasalu, I.C., Reddy, V.D. and Rao, K.V. (2008). Transgenic rice expressing *Allium sativum* leaf agglutinin (ASAL) exhibits high-level resistance against major sap sucking pests. *BMC Plant Biol.*, **8** : 102.
- Zhu-Salzmann, K.,** Shade, R.E., Koiwa, H., Salzman, R.A., Narasimhan, M., Bressan R.A., Hasegawa, P.M. and Murdock, L.L. (1996). Carbohydrate binding and resistance to proteolysis control insecticidal activity of *Griffonia simplicifolia* lectin II. *Proc Natl Acad Sci USA.*, **95**:15123-15128.

12th
Year
★★★★★ of Excellence ★★★★★