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Abstract The most important practical problems faced by everyone concerned with regard to BPH management are its extraordinary ability to develop insecticide resistance and also its ability to overcome the barrier of resistant varieties. A critical analysis of the whole of the information available till date reveals that nitrogen recycling and steroid biosynthesis mechanisms coevolved in BPH and its symbionts along with high plasticity in the multifunction oxidases, glutathione-S-alkyl transferases and other enzyme complex of BPH appear to be the most important physiological mechanisms that aid the destructive insect pest to realise high reproductive ability, there by greater diversity within the population and between the populations and finally establishing the insect biotypes capable of feeding on resistant varieties and also render the insecticides completely non-toxic within few years.

Keywords Insecticide; BPH; Resistance

Introduction

Rice Brown Planthopper, Nilaparvata lugens (Stal) (BPH) is the most destructive insect pest and also the most important yield limiting factor of rice crop today. We all know now that among all the tactics to manage the pest, use of insecticides is the most common method followed by utilization of resistant varieties whenever and wherever those are available. But it is also in the common knowledge of all the rice scientists and more importantly rice entomologists that BPH has already developed high to very high level of resistance to almost all the insecticides so far utilized. It is also well in the knowledge of almost all rice entomologists of the world that BPH could overcome the barrier imposed by resistant varieties wherever those were utilized. So the important point that drives us at this juncture is “Is there any relation between the varietal resistance breaking ability and insecticide resistance developing ability of BPH or not?” A critical look into the entire literature on BPH does not seem to have place to this important and ticklish question either in the form of direct experimentation or in the form of critical analysis from the existing literature. So this paper aims at fillin -g this important knowledge gap in our understanding about the physiological capability of BPH vis-à-vis its evolutionary position that is responsible for most pathetic position of rice cultivation in many areas of the world today.

Commonness of Varietal resistance and toxic action of insecticides towards BPH

Some varieties with resistance to BPH released from IRRI did perform well during the early days of 1970s in Philippines and also some South-East Asian countries, but later succumbed to insect attack. Studies conducted at IRRI and also in many other countries clearly demonstrated that BPH has the capacity to overcome varietal resistance within 6-7 generations (IRRI, 1975; Smith, 2005; Verma et al., 1979; Tanaka and Matsumura, 2000). Similarly BPH was very effectively controlled by neonicotinoids like imidacloprid and thiamehtoxam during early years of their use but became completely redundant and abandoned by farmers later. So is the case with regard to beuprofezin the insecticide thought to be the prestige of the industry at the time of introduction claimed to have no scope for resistance development in BPH because of its unique mode of action as an insect growth regulator cum chitin synthesis inhibitor. Thus we are standing almost at the dead end without knowing where to proceed further.

It is well known that the basic mechanisms in resistant varieties are antixenosis or non-preference for settling, feeding, oviposition etc., antibiosis reflected in varied ways of adverse effect on BPH biology in the form of reduced nymphal survival, enhanced nymphal period, reduced adult longevity and survival, lowered egg laying and so many other ways. The third aspect tolerance reflected with sustained crop growth and yield in spite of high BPH population. Today we know that all these original mechanisms coined by the initiators of the concept of host plant resistance are not that simple and each one is governed at genetic level by the production and sustenance of number substances each maintained at particular concentration at different plant growth stages by varied gene expressions in the plant. Again each of those substances have their role in a single or multiple ways influencing the whole of insect plant interactions finally deciding the extent of the ability of a variety to stand or not for BPH attack at a particular situation and place (Horgan , 2009).

With regard to the ability of BPH population in a region to overcome the toxic effect of an insecticide also the insect may basically develop ability to lower the penetration capacity of the insecticide through integument, render the chemical non-toxic through extensive metabolic degradation before it reaches the site of action located in nervous system in most cases or lower the sensitivity at the actual site of action (Krishnaiah, 2015). But when we compare the varietal resistance with insecticide toxicity there is some commonality along with certain distinct differences. Basic effect of both is similar where both render the insect incapable of feeding or directly kill BPH either slowly or more quickly. But the major difference between the two at basic level is, in case of insecticides the direct toxic effect of the active ingredient or its toxic metabolites exerts action on BPH while in host plant resistance, host plant reaction involving a series of developments in the plant system in terms of callose deposition, sieve tube sealing etc are also manifested along with release of certain chemicals involved in feeding inhibitory or toxic effects(Luna et al., 2011; Walling and Thompson, 2013). So the point of our discussion here is what basic features of BPH render the insect with such high physiological capability of overcoming insecticide toxicity and varietal resistance and what basic biochemical mechanisms are and could be responsible for both these types of capabilities in BPH.

Complementarity in BPH and its symbionts leading to total nitrogen recycling can play a decisive role in adaptability to insecticides and host resistance

If we view the whole of evolution in holistic manner, the organisms utilize nitrogen the most abundantly present gas in the atmosphere as the most crucial component in proteins the building blocks of fleshy material and elements in earth crust as base for hard structures like bones. But contrary to this general phenomenon, the insects along with other arthropods utilise only nitrogen containing substances even to build hard structures called exoskeleton. BPH is no exception to this generalization. That means if BPH has the ability to utilize nitrogen present in its body more efficiently than other insects, then certainly that constitutes the most important basic biochemical mechanism that aids in its genetic potential for very high reproductive ability.

From recent genomic analysis of BPH, this point is very clearly emerging (Xue et al., 2014). Normally ammonia, urea and uric acid are three excretory products that universally exist among all the phyla and so also in the class Insecta. If we critically see, ammonia is utilized as the most common excretory product in aquatic insects like other aquatic animals. This is because disposal of ammonia directly requires very high level of water all around to avoid its direct toxicity to the very organism involved. Urea is relatively safe and freely soluble in water. Therefore, most of the terrestrial insects and also terrestrial organisms including humans use urea as the common excretory product. However, only the insects which do not have access to water and contain almost no free water in the food like those in the deserts and those insects feeding on hard tissues like dead wood use uric acid as their nitrogenous excretory product very similar to birds. This is an evolutionary mechanism to conserve the scarce resource of available water because uric acid is almost insoluble in water and hence directly disposed off along with faeces. Thus, in case of BPH whose diet, the rice phloem-sap containing copious amount of water in it, logically there is no practical need of any production of uric acid as a nitrogenous waste product for BPH. In spite of this, BPH produces uric acid in its body probably as the most energy efficient way of storing the excretory products and yeast like symbionts present in fat body of BPH (YLS) utilize that waste product for synthesis of essential amino acids for BPH because BPH per se cannot synthesize essential amino acids due to lack of concerned genes in its genome. Further, the whole of genome of BPH and YLS and other symbionts are so complimentary to each other that those contain all essential sequences for encoding the whole of nitrogen recycling process. Thus the net loss of nitrogen from BPH body seems to far less compared to other similar sap sucking insects. This probably is one of the most important biochemical reasons behind the high reproductive potential of BPH to complement its innate genetic potential.

This high reproductive ability by utilizing a given food source naturally enable the insect to have better diversity within the population and thereby among different populations. The most important point we have to note here is, once an insect gets better ability to overcome a resistant variety or to nullify the toxic effect of a particular insecticide, naturally any of those two factors existing under field conditions act as a sieve to remove the susceptible individuals and high innate reproductive ability of BPH quickly establish the resistant individuals. Thus nitrogen recycling complimenting ability of BPH and its symbionts appear to be the most decisive common factor to overcome the host plant resistance and also the ability to develop insecticide resistance in BPH.

Complementarity in Steroid biosynthesis between BPH and YLS can be an effective factor in conferring insecticide resistance and also host plant resistance breaking capacity:

Sterols are essential components in all eukaryotes or multicellular organisms both plants and animals. Sterols serve four critical functions in insects: (1) they are important components of cellular membranes, modulating membrane permeability, fluidity, organelle identity, and protein function (2) they are precursors for many hormones including 20-hydroxyecdysone and its precursor ecdysone (3) they play a role in regulating genes involved in developmental processes and (4) they act as signalling molecules in host selection and other environmental factors. During the course of evolution, insects as a whole including BPH have lost the genes that encode for the enzymes involved in synthesis of squalene which is the most essential precursor for steroid biosynthesis. Hence, BPH like other insects requires external source for sterols. But phloem sap of rice plant on which BPH feeds is a poor source of cholesterol or other sterols. Hence, BPH has started getting the cholesterol or other steroids from yeast like symbionts (YLS) present in mycetocytes in egg and in mobile stages (Pang et al., 2012). From cholesterol or other steroids ecdysone and 20-hydroxyecdysone are synthesized in thoracic glands of BPH with the help of its own enzyme complex involved in hormonal regulation.

Very critical and most comprehensive look at the whole of information on mode of action of buprofezin based on the papers published in 1980s (Asai and Fukada , 1983; Asai et al.,1985; Kobayashia et al., 1989) along with the most recent information generated by Xue et al., (2014) as a part of their study on BPH genome along with the genomes of the YLS reveals an important point. Complete complementarity between BPH and YLS is essential for synthesis and functioning of cholesterol and other steroid hormones including ecdysone and 20hydroxy ecdysone required for many functions including moulting and ovarian development in BPH. A disturbance in this vital link of steroid metabolism has been deduced to be the key element in the mode of action of buprofezin in BPH. A critical look into this aspect in future research on buprofezin resistance in BPH has been focussed to be the most vital area to be attended to understand this important aspect and to develop strategies for buprofezin resistance management in BPH (Krishnaiah, 2015).

Although a similar comprehensive analysis and understanding has not been attempted anywhere in the literature on the role of steroids in host-plant resistance to BPH and the ability of the insect to overcome this barrier, some interesting information is available from Japanese literature. Using a pair of isogenic japonica rice lines, 80R (resistant) and 74S (susceptible), developed through repeated selection of F11 through F19 plants from an F2 (Hoyoku × Mudgo) × Kochikaze cross (therefore containing the Bph1 gene), Shigematsu et al (1982) determined that aerial plant parts of 80R contained beta-sitosterol, stigmasterol, and campesterol in larger quantities than 74S. Furthermore, honeydew collected from planthoppers feeding on 80R had cholesterol and beta-sitosterol. In vitro studies using these steroids with BPH revealed that 50 ppm of beta-sitosterol and 15% sucrose caused total inhibition of sucking by BPH in parafilm tests and other sterols also showed almost similar effect.

Further sterols along with waxes constitute important physical barriers for mechanical prevention of BPH feeding. In recent studies by Seo et al., (2009) on resistance-breaking ability of wild BPH on resistant rice varieties in Korea, nymphal survivorship test indicating the adverse effect of toxicants and antifedants present in resistant varieties and electrical penetration graph (EPG) study to understand the mechanical obstruction for stylet penetration by BPH showed certain interesting points. survival rates of BPH most recently collected from rice fields during 2007 could almost overcome the antibiosis effect of resistant varieties Gayabyeo (Bph1 + bph2) and Rathu Heenati (Bph3) compared to the mild type of BPH collected during 1980s and reared continuously on susceptible varieties. But EPG studies have clearly revealed that BPH collected from rice fields during 2007 could overcome the mechanical barrier for feeding to some extent but still faced stiff adversity in stylet penetration into resistant varieties compared to susceptible varieties. This indicates that ability of BPH as a species to overcome the barriers in steroid metabolism is relatively more difficult for the insect than its ability to adopt for detoxification of toxicants and nutritional deficiency factors acting as factors of antibiosis.

Thus development of abilities in BPH to cope up adversities due to insecticides and host resistance with regard to steroid metabolism also serve as a common link in the ability of BPH to overcome these twin adversities for expression of its innate potential under field conditions. A lot of future research is needed to understand this complex phenomenon.

Mixed function oxidases or multifunction oxidases (m. f. o.) can play an effective role in insecticide resistance and host resistance break-down capabilities of BPH

As it is well known, that in case of insecticide resistance development in BPH, detoxification of active ingredient into nontoxic moieties is the major important contributing factor. Same is the case in varietal resistance break-down when the host resistance is mainly contributed by a toxic substance in the resistant varieties.

The first step of detoxification of an insecticide in coelom of BPH like in many other insects is oxidation and dehydrogenation followed by hydroxylation, because most of the insecticide molecules are lipophilic and they can be subjected to further degradation more easily through this route. This step of oxidation in most molecules is more effectively achieved by enzymes present inside the fat-bodies which are also located inside the coelom of BPH body. These fat bodies contain more effective oxidizing enzymes called mixed function oxidases or multifunction oxidases (m. f. o.). These fat bodies of BPH are analogous to liver of higher animals including man. This m. f. o. is usually membrane bound enzymes located in microsomes or ribosomes of fat body cells. This m. f. o. during later times is also called as cytochrome P450 mono-oxygenases due to absorption maxima at 450 nanometers for the cytochrome containing these enzymes. Although the main function of these m. f. o. is to oxidize the lipophilic insecticide as a first step to convert it into a metabolite that can more easily be transformed into a hydrophilic molcule(s), which most of the times are far less toxic than parent compound or even completely non-toxic to BPH. Further these hydrophilic molecules can be eliminated from insect body more easily through normal excretory function. Apart from oxidation, it has also been found in many instances that m. f. o. can degrade lipophilic insecticides through other modes of degradation like hydroxylation, break down at ester linkage etc. But, the major mode of degradation is through first step oxidation and hence their name mixed function or multifunction oxidases.

These are the enzymes which have come into existence during the course of evolution to enable the insects to detoxify any chemical present in the plant-food which can cause some disturbance to its normal physiological functioning of the body resulting in any type of adverse effect on survival and multiplication. However, magnitude of these enzyme systems and intensity of their activity in BPH seem to be very well correlated with its evolutionary position and host specificity. BPH appeared to have lost many of the original P450 genes during its adaptation from Leersia hexandra to rice in the past 2.5 lakh years of its evolution and host adaptation to rice in swamp environment (Jones et al., 1996). At present BPH has been found to have only 67 genes encoding for P450 enzyme systems in its genome compared with other similar phloem feeders like pea aphid Acyrthosiphon pisum with wider host range retaining 83 genes related to P450 (Xue et al., 2014).

These m. f. o can handle variety of substances, but the major tactic of these enzyme systems is their rate of functioning is much slower than other normal enzyme systems involved in digestion, absorption and utilization of food for body growth and other vital functions. Thus m. f. o. are regarded as the protecting enzyme systems for insects as much as these type of enzyme systems present in higher animals like man in liver are responsible for degrading medicines and other foreign substances introduced into human or animal systems.

The most important molecules among organophosphates that have been very extensively used against BPH during 1980s are malathion and fenitrothion for which there was very high level of resistance development in BPH in China and Japan. In fact the main reason for their usage was their mammalian or human safety compared to other organophosphates. In case of fenitrothion the methyl moiety attached to the phenyl ring is the only thing that makes it different from methyl parathion but rendering the molecule some 50-100 times safer to humans. The main enzyme systems that are responsible for this phenomenon are m. f. o. The m. f. o. in mammals are capable of very quickly oxidizing the methyl moiety in fenitrothion to carboxyl group while insect systems including BPH fat bodies are not that much faster in executing this reaction. For malathion, the carboxyl ester groups in the side chains of the molecule are broken down very fast in human systems or in other higher animals, while in insects including BPH the degradation is very slow. Thus malathion has much inbuilt safety to mammals. But interestingly, when BPH developed resistance to fenitrothion, resistant strains had developed the similar mechanism as mammalian systems to convert the methyl moiety to carboxyl group at a faster rate rendering the molecule almost nontoxic to BPH in resistant strains. In case of malathion also, the resistant strains developed the systems which can break carboxyl ester linkage very fast which is again similar to mammalian systems thus rendering malathion almost nontoxic in resistant BPH strains in Taiwan (Sun and Chen, 1993; Chen and Sun 1994).

This phenomenon of detoxification of insecticides by m.f.o. applies to almost all groups including OPs, carbamates, neonicotinoids, buprofezin and any other future groups that are likely be developed and will be used.

In case of varietal resistance, the actual role of m.f.o in degrading the toxic materials present in resistant varieties is not well delineated and understood. The main reason is actual biochemical characterization of varieties resistant to BPH has been done in very few cases. Even among those the actual level of toxicity of the molecule or molecules could not be determined quantitatively for varied reasons of practical limitation. That does not mean that m.f.o. existing in BPH is not involved in detoxification of the toxic chemicals conferring host plant resistance in a resistant variety. Further in most cases of varietal resistance to BPH along with toxic chemicals other factors like mechanical obstructions for feeding and nutritional factors may also be involved in the same variety.

However, in very few cases of involvement of toxic secondary chemicals in BPH resistant varieties and the role of P450 within BPH system in degrading those toxicants has been demonstrated. When BPH feeds on the resistant Chinese variety B5 (containing Bph14 and Bph15 genes) a BPH gene (Y342) encoding for P450 is activated within the insect system (Yang et al 2005; 2006; 2007). Yoshihara et al (1980) observed higher oxalic acid content in Mudgo (Bph1) which has exhibited feeding inhibition in parafilm bioassays and BPH biotype1 adapted for feeding on Mudgo could probably develop ability to detoxify oxalic acid.

Stevenson et al (1996) found that in the phloem of BPH resistant rice varieties Rathu Heenati, BG300, and BG379/2, the phloem sap has been found to contain higher concentrations of C-glycosidic flavonoids like schaftoside, isoschaftoside, and apigenin than susceptible varieties. All these flavonoids existing as glycosides in resistant varieties have been found to exhibit very high antifedant activity on BPH when used along with 20% sucrose solution in parafilm feeding sachet tests (Stevenson et al, 1996). Bing et al (2007) isolated the flavonoid 5, 7, 4′-trihydroxy- 3′, 5′-dimethoxyflavone (tricin) from IR36 the BPH resistant variety with the bph2 gene. Tests with artificial diets and treated rice seedlings showed that tricin can exhibit antibiotic effects on BPH through lowered nymphal survival and feeding as well as reduced feeding and egg-laying in adults.

If we see some of the most modern insecticides like pymetrozine, the insecticide has been found to exhibit only antifedant activity. If we critically analyze the whole of insecticide use scenario at present, pymetrozine is the only insecticide for which there are no reported cases of resistance development in BPH. But based on the evidence already available in case of chemicals present in BPH resistant varieties with antifedant activity (He et al., 2011) and the role of m.f.o. present in BPH in degrading those chemicals, it is no wonder if we predict that BPH will certainly develop resistance even to pymetrozine the only hope of rice farmers existing at present.

Glutathione-S-alkyl transferases (GST) another major enzyme system in insecticide detoxification can also play a role in degrading toxic substances involved in varietal resistance to BPH:

Another, most important group of enzymes that aid in degradation and detoxification of many insecticides either fully or partly is glutathione-S-alkyl transferases. The main mode of action of this group of enzyme systems is transferring an alkyl group which in majority of the cases is methyl group and sometimes ethyl and rarely other alkyl groups with higher carbon number. In case of most organophosphates which have undergone extensive metabolic studies possess alkyl groups attached to phosphorus atom in ester linkage, when the alkyl groups are moved away from the parent compound by these glutathione-S-alkyl transferases that immediately renders the molecule nontoxic. Since the enzyme system involved in the transfer of alkyl group has glutathione molecule with sulfur moiety in the active site, the name of the enzyme systems has been called as glutathione-S-alkyl transferases. Almost same is the case in many other insecticide groups like carbamates, neonicotinoids etc. In case of neonicotinoids it must always be remembered that insensitivity of site of action i.e. nicotinic acetyl choline receptors is so far considered as the only mode of resistance development in BPH. But contrary, the latest studies have shown involvement of metabolic degradation also as the major mechanism based on studies with direct field collected specimens of BPH (Puinean et al. 2009; Wen et al. 2009). Hence the role of both m. f. o. and GST in neonicotinoid resistance in BPH cannot simply be brushed aside as redundant.

In case of resistant varieties the studies on biochemical characterization itself is the greatest limiting factor in understanding the role of GST in detoxifying the toxic components in resistant varieties. Nevertheless we should not forget the fundamental fact that GST along with m. f. o. are general enzyme systems which are universal in their occurrence and not confined to insects alone and hence these are not specific to BPH. Again the fundamental purpose of GST along with m. f. o. are a part of counter defense mechanisms evolved by BPH to enable it to continue to utilize rice its only host by breaking barriers imposed by varietal resistance even in their wild form.

Interestingly similar to P450 enzyme systems GSTs in BPH also had lower number than the polyphagous A.pisum indicating the loss in diversity due to coevolution of BPH along with rice towards its mono-phagous nature. This is another indirect indication of the involvement of GST as major detoxifying enzyme systems in BPH for toxicants and antifedants present in resistant rice varieties. Thus we could see a commonality in the GSTs as another biochemical mechanism responsible for insecticide resistance and host plant resistance breaking ability of BPH.

Esterases including phosphatases can also play a role in degradation of both insecticides and toxic chemicals present in resistant varieties to BPH:

When BPH starts feeding on rice plants treated with insecticides more specifically in case of true systemic compounds like neonicotinoids, the movement BPH inserts its stylet into the plant; the insect also injects its saliva into the plant. If we critically observe the saliva of BPH it is literally a biochemical factory containing varied enzyme systems. Most of those enzymes are the ones involved in aiding the insect in continuous feeding on phloem sap, some of the enzymes involved in partial digestion of the phloem sap before sucking through stylet into the digestive system. When the insecticides are taken inside the digestive system of BPH those insecticides are also subjected to metabolic degradation in a variety of ways. When the insecticides reach the coelom which is filled with BPH blood the insecticide degradation can occur very extensively before the toxicant reaches the nervous system where the site of action of most insecticide groups lie.

Regarding the type of enzyme systems that handle the insecticides during all the above processes in BPH, there are hundreds of types of esterases, whose names are coined depending on the type of ester linkage. Those are involved in breaking like phosphate involving linkage called “phosphatases”, in case of carboxyl ester linkage those are termed as “carboxyl esterases”, carbamyl ester linkage involved enzymes are called “carbamylases” and so on apart from those involved in direct metabolism of nutritious substances. In studies on the development and mechanism of insecticide resistance in BPH, with compounds belonging to different groups like OP s (malathion) and carbamates (MTMC or metolcarb), which are almost similar in their mode of action, it was observed that malathion resistance was caused by high degradative activity of enzymes converting malathion and malaoxon to nontoxic products, while metolcarb resistance was caused by low sensitivity of acetyl cholinesterase. Among the synergists tested along with these insecticides to block the degradative mechanism, 2-phenyl-4 H-l, 3,2 - benzodioxaphosphorin 2-oxide and 2-phenoxy-4 H-l, 3, 2 benzo-dioxaphosphorin 2-oxide were most effective (Hama and Hosoda , 1983; Endo et.al., 1988). High esterase isoenzyme activity was noticed in BPH resistant organophosphate insecticides than in the susceptible strain in Korea (Kim and Hwang, 1987). Esterase activity in BPH treated with diazinon, fenitrothion or BPMC [fenobucarb] was not decreased in the resistant strain but was markedly decreased in the susceptible strain, as compared with untreated BPH specimens, suggesting that esterase isoenzymes continued their breakdown activity in OP resistant BPH strains but such capability was absent in susceptible strains. This speaks on the changed quality of esterase isoenzyme systems along with development of resistance to organophosphate compounds. Further this phenomenon was observed in F1 hybrids there by suggesting very typical Mendelian laws of inheritance.

A a number of chemicals present in resistant rice varieties and exerting toxic or antifedant activity against BPH could be subjected to degradation and converted to nontoxic moieties by esterases or other types of enzyme systems present in saliva of BPH and also similar enzymes present in coelom of BPH body. But a detailed study is available in case of benzyl benzoate a chemical that is present in watery lesions of some of the japonica varieties. In case of the Japanese rice variety Reiho exhibiting very high level of egg mortality of WBPH it has been proved to be due to the presence benzyl benzoate.

Benzyl benzoate has been shown to be highly toxic to WBPH eggs in vitro also. In further biochemical analysis it has been shown that Benzyl benzoate is synthesized through a series of biochemical reactions in WBPH induced watery lesions in Reiho variety (Seino and Suzuki, 1997; Seino et al., 1996). Eggs of WBPH develop eye spots within 4 days and presence of benzyl benzoate completely inhibits egg development before eye spot formation. Hence, five days after oviposition, an egg with eye spots can be considered as a viable egg whereas an egg with-out an eye spot is considered dead. Benzyl benzoate is not detected in intact plant tissue and non-watery lesions suggesting that Japanese rice cultivars have an induced resistance to WBPH oviposition. A detailed genetic analysis of this practically important trait designated as Ovc present in Japonica variety Asominori with reciprocal genetic backgrounds of a non-ovicidal Indica variety IR24 revealed that four ovicidal quantitative trait loci (QTLs), qOVA-1-3, qOVA-4, qOVA-5-1 and qOVA-5-2 were responsible for variability of this trait among isogenic lines (Yamasaki et al., 2003).

However, the detailed studies on the influence of different enzyme systems present in BPH on metabolism of benzyl benzoate is not available due to practical limitations and also due to the reason that the studies are not essentially required.

Summary and conclusions

Brown Planthopper, *Nilaparvata lugens* (Stal) (BPH) the most important insect pest of rice has developed high level of resistance to almost all the insecticides so far used and also could overcome the barrier imposed by many resistant varieties. So it is important to analyse that "Is there any relation between the varietal resistance breaking ability and insecticide resistance developing ability of BPH or not?"

The commonality of insecticides and resistant varieties is that both render the insect incapable of feeding or directly kill BPH either slowly or more quickly. But in case of insecticides the direct toxic effect is manifested by the active ingredient or its toxic metabolites, while in resistant varieties host plant reaction involving a series of developments in the plant system in terms of callose deposition, sieve tube sealing etc also occur along with release of certain chemicals involved in feeding inhibitory or toxic effects.

Among different factors, complementarity in BPH and its symbionts leading to total nitrogen recycling appear to play the most important and decisive role in adaptability of BPH to insecticides and resistant varieties.

A disturbance in the vital link of steroid metabolism between BPH and YLS which is essential for synthesis and functioning of cholesterol and other steroid hormones including ecdysone and 20hydroxy ecdysone has been deduced to be the key element in the mode of action of buprofezin in BPH.

Cytochrome P450 mono-oxygenases present inside the fat-bodies of BPH which are well known for insecticide detoxification, there by insecticide resistance development in BPH have been evolved primarily to overcome toxic substances in host resistance and are involved in break-down of resistant varieties by BPH.

Glutathione-S-alkyl transferases (GST) well recognized in insecticide detoxification can also play a role in degrading toxic substances involved in varietal resistance to BPH.

Saliva of BPH containing varied enzyme systems aids in continuous feeding on phloem sap as well as partial digestion of the food. These enzymes also play important role in degradation of systemic insecticides ingested along with the sap. In addition, a variety of enzymes present in BPH blood inside the coelom degrade both insecticides and toxic substances present in resistant variety. Benzyl benzoate synthesized through a series of biochemical reactions in WBPH induced watery lesions in some Japanese varieties is a typical example of this phenomenon.

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