

parable to the best institutions in the world. It is high time that adequate measures are put in place to adopt procedures for faculty hiring as in the US. Hiring of faculty should involve proper planning, search and day long exposure and interaction to provide opportunity to the candidates to know about the institution and the people working there and vice versa. A threshold level of criteria in terms of publications in international fora and cumulative impact factor is a must as the first step of screening^{5,13}. This would automatically eliminate the frivolous candidates and those making an effort for back-door entry. It is time to remember what Winston Churchill said: 'The era of procrastination, of half-measures, of soothing and baffling expedients, of delays, is coming to a close. In its place we are entering a period of consequences'. A silver lining has come in the form of an announcement about some sweeping measures by the honorable Prime Minister, which include a quantum jump in

investment in science education and research, and a range of schemes to attract students and replenish the shrinking pool of scientific personnel¹⁴. Thus men and women in the laboratories can look forward to qualitative as well as quantitative changes in their lives, sooner than later.

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***Bt* resistance and monophagous pests: Handling with prudence**

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Bacillus thuringiensis (*Bt*)-based insect pest-resistant transgenic crops have become a commercially successful and viable product in agricultural biotechnology globally. Both the area under *Bt* crops and demand for *Bt* crop seeds are increasing. In India, the area under *Bt* cotton, the first ever commercial transgenic crop, has shot up from nearly 30,000 ha in 2002 to 9.5 mha in 2007, constituting nearly 66% of the total cotton area with an expected output of 31 million bales. From a mere three *Bt* cotton hybrids in 2002, nearly 135 *Bt* cotton hybrids are under consideration for commercialization with a projection hinting further expansion in area and productivity. In cotton, *Bt* toxin is directed against the cotton bollworm, *Helicoverpa armigera* (Hubner). This and many other pests are polyphagous (attacking multiple crops) and have more than one host crop. For example, *H. armigera* has more than 200 host plants on which it can feed, lay eggs, complete its life cycle and multiply. Various tactical methods are

deployed for delaying the development of resistance to *Bt* in insect pest populations (Table 1). However, certain issues still remain to be answered. If the cotton is *Bt* transgenic, the pest has options of invading non-*Bt* cotton and other crops. Not all pests are polyphagous. Pests like the cabbage diamondback moth (*Plutella xylostella* L.; Plutellidae, Lepidoptera), rice stem borer (*Scirpophaga incertulas*) (Walker; Pyralidae, Lepidoptera) and the brinjal shoot and fruit borer (*Leucinodes orbonalis*; Guenee; Pyralidae, Lepidoptera) are monophagous and do not have alternate host crops. So far, all the research and field experiences with regard to *Bt* technology and possible emergence of resistance to *Bt* in pests have concentrated on polyphagous pests, especially *H. armigera*^{1,2}. The stochastic model 'Bt-Adapt' developed at the Central Institute of Cotton Research, Nagpur, to understand and predict the rate of resistance development of *H. armigera* to *CryIAC*-based *Bt* cotton is definitely not applicable per se to monophagous pests³. Be-

sides, unfortunately, there are hardly any studies with regard to *Bt* rice–*S. incertulas* and *Bt* brinjal–*L. orbonalis* systems. How are monophagous pests different from their polyphagous counterparts with respect to emergence of resistance to *Bt*, selection pressure and genetic dynamics of alleles in their populations and management of resistant types? How stringently are they monophagous? What are the molecular and physiological mechanisms that drive the development of resistance? How effective are the deployment tactics in reality? These and other questions need a thorough generation, analysis and interpretation of data, as a forewarning step, to ensure that Indian agriculture will be prepared to face in the imminent possibility of emergence of *Bt* resistant pests, polyphagous or monophagous, due obviously to the recent spontaneous changes we are all witnessing, of the dominating demography of cultivation of GM crops. The exigency of the problem is hastened by the recent observations of *Bt* cotton

Table 1. Methods to address *Bt* resistance development in insect pests

Method	Genetic or agronomic (reason)
Refugia	Agronomic (to maintain susceptible insects)
Ultra high dosage	Genetic (to kill heterozygous resistant insects)
Moderate dosage	Genetic (to ensure survival of fraction of susceptible insects)
Tissue- or temporal-specific <i>Bt</i> expression	Genetic (to reduce selection pressure)
Mixing <i>Bt</i> and non- <i>Bt</i> seeds	Agronomic (to maintain susceptible insects)
Gene pyramiding	Genetic (to severely reduce emergence of resistant alleles)
Mixture of toxins	Genetic and agronomic (to maintain susceptible insects)
Use of newer and more potent <i>Bt</i> genes	Genetic (to address resistance <i>de novo</i>)

affected by hitherto secondary pests, including sucking pests.

Globally, there are few reports indicating the development of resistance in insect pests against *Bt*. Resistance has been documented under laboratory conditions. However, in the field only one pest, diamondback moth, has evolved resistance to *Bt* sprays and none has evolved resistance to *Bt* crops. In India, so far the track record of *Bt* technology is better with no reports on field resistance to *Bt* cotton. The build-up of *Bt* resistance may be either invisibly slow or perhaps non-existent. Despite this success, the incredible and highly plastic adaptive ability of the insects to the evolutionary challenges means that resistance remains a crouching threat⁴.

Key factors that delay resistance to *Bt* crops in the field include refugia of non-*Bt* crops, including size of refugia (diluting resistant alleles), recessive inheritance of *Bt* resistance, degree of dominance of resistance, low initial frequencies of resistant alleles, fitness costs, high toxin doses, gene flow and the very nature of incomplete resistance. Other factors like type of selection (hard or soft), accelerated fitness costs of adaptation, spatial distribution structure and abundance of defended hosts and refuges, magnitude of search cost coefficient, habitat preference and population adaptive index can also affect adaptation of the pests. But in the absence of even empirical models, these are just assumptions and one or more of these assumptions may be violated in pest populations challenged with *Bt*. Basically, both the expression and durability of insecticidal genes, including *Bt*, depend on the category of resistance, the genotype of the pest and the interaction between the cultivar, pest and environment. Appearance of *Bt* resistant biotypes of pests is often in response to the high levels of antibiosis (vertical gene) resistance. Biotypes form in much the

same way that pests develop resistance to chemical insecticides, by the selection of individuals with behavioural or physiological mechanisms that enable them to survive exposure to the *Bt* toxin.

Notwithstanding, each of these factors can by itself also become responsible for the emergence of resistant pests if proper population genetic studies are not undertaken. Strict compliance of 20% refugia by both the private companies and the farmers is questionable, at least in India. Also, it is doubtful if the *Bt* cotton growers indeed take up external pest control measures, which otherwise would ensure obliteration of *Bt*-surviving larvae. Carefully developed population genetics models indicate that *Bt*-free refuges would permit susceptible insects to survive and swamp-out resistant variants that might emerge from the pest population feeding on *Bt* plants in nearby fields. As the area under cotton cultivation is increasing exponentially, it becomes increasingly impossible to expect nearby fields to act as refugia as larger tracts come under the cultivation of *Bt* crop, exemplifying gene monoculture. Smaller areas of non-*Bt* crop in the midst of vast areas of *Bt* crops cannot sustain requisite minimum size of susceptible insect populations to act as refugia. Insect resistance to *Bt* is partially or completely recessive in most laboratory-selected strains and in the field-selected strains of diamondback moth, the first insect to evolve resistance to *Bt* in open populations. Recessive alleles, once created or introduced in the population, are difficult to be removed. The frequency of recessive alleles observed in the population results from a delicate balance between creation of resistant genotypes by mutation and selection against such resistant mutants when *Bt* (selection pressure) is not present. Large-scale cultivation of *Bt* cotton and other crops can maintain the selection pressure, resulting in tipping the

equilibrium in favour of development and maintenance of *Bt*-resistant alleles in the populations. Even though initially the frequencies of resistant alleles in any population are low, they may increase due to continuous operation of selection pressure on larger areas. Part of this problem can be addressed by simultaneous deployment of chemical pesticide sprays in the non-*Bt* refuges and *Bt* crops to take care of any remaining *Bt*-resistant insects.

These concerns get complicated when we address the monophagous pests. If a female insect's fecundity is limited by the time available for oviposition, then a polyphagous pest will have a higher fecundity than its monophagous cousin, because it can find and oviposit on more acceptable plants per unit time. This effect is essentially a search cost associated with behavioural specialization (host avoidance). Also, the problem of spread and gene flow of *Bt*-resistant alleles can be high, particularly in polyphagous pests which may later have an increasing source of pre-adapted immigrants entering the *Bt* cropping systems. Monophagous insect pests, on the other hand, possess reduced relative host abundance due, in part, to the lack of habituation to non-host plants. When confronted with the incompatible *Bt* transgenic hosts, the operative selection pressure tends to be significantly higher against the population. These pests mostly exhibit reinforced development of direct counter-adaptation in the form of neutralization of the defensive innovation (physiological adaptation)⁵. This can concomitantly increase the mutation rates and selection of favourable resistant alleles, however small the population is. As we know, selection increases or decreases the chance of fixation of alleles according to whether the new mutant allele is favourable or unfavourable in the population. Even though a great majority of mutant alleles are ex-

pected to be deleterious, in the case of *Bt* resistance, the mutation becomes favourable, thus increasing fitness. Such resistant alleles in the monophagous insects tend to be fixed in the population at a faster rate due to the artificially intensified selection through *Bt* crops. The selection can shift from stabilizing type to directional type due to the continuous selection intensity operative against the population. The genetic load operative on the pest population agreeably increases because of the concomitant genetic death of many individuals in the pest population due to *Bt* toxicity and lack of alternate host crops. The adaptive peak landscape tends to become skewed towards more *Bt*-resistant alleles. Besides, migration of a new resistant allele into a population that already has an altogether different resistant allele can create additional problems, especially in *Bt* gene pyramiding programmes, since unless newer *Bt* genes are used in pyramiding, mere stacking of *Bt* genes that are already in the field (and against which if resistant alleles already exist) tends to be futile.

Briefly, there is an urgent need of systematic investigations on the population genetic structures of *Bt* resistance with the recent wave of large-scale cultivation of *Bt* crops. The history of the development of resistance to chemical insecticides contains frequent episodes in which resistance has occurred through mismanagement, and often over-use of insecticides by a few individuals (which may have resulted in the *Bt* resistance

developed by diamondback moth in Hawaii). Safer and sensible use of *Bt* transgenics is in the hands of farmers with varying (often low) levels of skills in India. Like any other chemical insecticide, *Bt* transgenics-based pest management is only as good as those who use them. The problem is confounded in the case of monophagous pests, which do not have alternate hosts due to which selection pressure response becomes aggravated towards increased frequencies of resistant alleles. Long-term studies, including baseline susceptibility, spatial/temporal distribution of refugia, population adaptive index and genome-wide sampling of insect populations should be integrated with pest biology. Potential flow of *Bt* genes into wild and feral host plants and *Bt*-resistant alleles into susceptible but closely related pest populations also demands thorough investigation. Fate of natural enemies in *Bt* fields also demands a consideration. 'Population genomics' and 'Ecogenomics' approaches should form an integral part of the *Bt* resistance studies. This will help us prepare ourselves with operational procedures and tools to develop strategies for *Bt* presentation to pests and retaining *Bt* susceptibility in pests, and also address the imminent problems of *Bt* resistance in pests⁶. The durability of first (single gene) and second (pyramided genes) generation *Bt* crops will be most dependent on the education of end-users about practices which will ensure the continued susceptibility to *Bt*⁷. Sensitive monitoring of resistance and sensible deployment of tac-

tics⁸ are needed by scientists, farmers and environmentalists. Handling with caution, judiciously applying the precautionary principle and exercising moderation in regard to *Bt* transgenic technology where the pests addressed are especially monophagous, are both mandatory as well as prudently sensible.

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