Harnessing transgenerational plant immunity

Soil, microbes and all living beings including humans are being victimized from the current pesticidal regime and are looking forward to a much needed change in the current agricultural practices. Young children are particularly seen to be vulnerable to the harmful effects of pesticides[1]. Hence, alternatives to synthetic pesticides are being sought[2,3]. Strengthening the host innate immunity is seen as a potential way to lower the pesticide usage in agricultural fields[4]. A unique defence state can be induced in plants by exposing them either to less virulent necrotrophic pathogens/beneficial microorganisms or resistance-inducing compounds. Such plants possess amplified defence responses when they are further attacked with biotic agents or challenges posed by abiotic factors. The state of enhanced capacity to activate stress-induced defence responses has been called the 'primed' state of a plant[5]. The primed state in *Arabidopsis thaliana* was found to be fully functional even in the next generation without additional priming[6]. Plants being sessile organisms cannot communicate with their descendents regarding the potential threats surrounding them. Hence, plants must have evolved to utilize this priming phenomenon to communicate with their descendents. The response of the descendents of *Arabidopsis* plants that had been either primed with β-aminobutyric acid (BABA) or with an avirulent isolate of the bacteria *Pseudomonas syringae* pv. *tomato* (*Pst*avrRpt2) showed a faster and higher accumulation of transcripts of defence-related genes in the salicylic acid signalling pathway. The descendents also showed enhanced disease resistance upon challenge inoculation with a virulent isolate of *P. syringae* as well as against the oomycete pathogen *Hyaloperonospora arabidopsidis*. Further priming of the offspring with the same agents triggered even higher degree of defence responses. Similarly, when *Arabidopsis* and tomato (*Solanum lycopersicum*) plants were challenged with either caterpillar herbivory or methyl jasmonate during the vegetative growth stage, subsequent induction of resistance was observed to be transgenerational and jasmonic acid-dependent in both species[7]. The effect persisted for two generations in *Arabidopsis*, and inheritance of resistance in both the Brassicaceae and Solanaceae families further indicates that this trait is widely distributed among various plant species.

Evolutionary trends indicate that transgenerational epigenetic inheritance is a way to communicate with the offspring[8]. Epigenetics is the heritable change in gene activity without any alteration in the DNA sequence. Epigenetic changes in genetic material may take place due to changes in DNA methylation patterns, histone modification and activities of small interfering RNAs (siRNAs). These changes thus, heritably and reversibly modify the expression of genes without causing any change in the nucleotide sequence of DNA. These epigenetic changes can exist for the entire duration of the life of a cell encompassing cell divisions, and may also sustain in several subsequent generations[9]. Several reports have demonstrated epigenetic changes taking place in animal biology. One of the best examples is the cellular differentiation that takes place during morphogenesis, where the totipotent stem cells become various pluripotent cell lines of the embryo, and differentiate into neurons, muscle cells, epithelium, endothelium of blood vessels, etc.[10]. Differential morphogenesis takes place through activation of some genes and inhibition of the others in different pluripotent cells. In a similar way, significant amount of evidences is gathered in plant biology as well in relation to inducible transgenerational epigenetic changes. Such evidences are growing exponentially with every passing year. A successful illustration demonstrated that disease pressure by *P. syringae* pv. *tomato* DC3000 (*Pst*DC3000) can be inherited epigenetically in *Arabidopsis* and the offspring showed enhanced plant immunity against further challenge with the pathogen. Challenge with *Pst*DC3000 activated salicylic acid (SA)-inducible defence genes and suppressed jasmonic acid (JA)-inducible genes, and the offspring showed enhanced resistance against the (hemi)biotrophic pathogens *Hyaloperonospora arabidopsidis* apart from *Pst*DC3000. Further, it was reported that the transgenerational defence response requires signal transduction via the *NPR1* gene[11]. Recent studies further revealed that certain enzymes such as HDA6 are essential for regulation of gene activity and genome maintenance in plants[12].

Induced transgenerational epigenetic changes in plants could thus be harnessed to improve agricultural crop production and protection (Figure 1). More so, by developing easy and suitable techniques to bring desired changes in plants through this biological phenomenon. Epigenetics has also been looked upon as a potential tool to understand plant functional genomics as it has the potential to decipher and impart stress adaptive potential in agricultural crops as well as in other plant species[13]. Harnessing of epigenetic phenomenon has been relatively common in crop production. Studies on evolutionary biology point out that heritable changes such as plant flowering

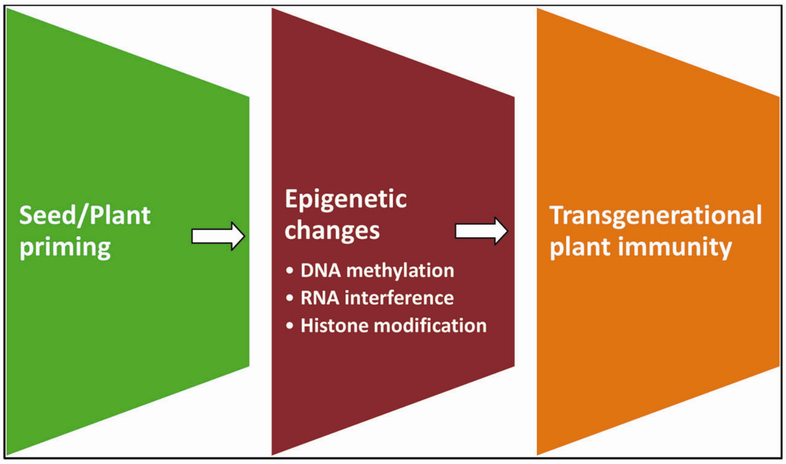

Figure 1. Process of transgenerational plant immunity development.

time are the result of epigenetics alone[14]. Since flowering time is one of the most important characteristics in breeding programmes, epigenetic studies could be incorporated while selection of early flowering germplasm for breeding short duration cultivars. Recent reports on inducible transgenerational epigenetic changes in plant DNA to bring desired changes in the expression pattern of some genes provide us an opportunity to play with and bring out desired heritable changes in target crops for both production and protection. However, additional studies are required for thorough understanding of the epigenetic transgenerational regulation in plants. Better understanding of the phenomenon will help in developing strategies to regulate plant genes through epigenetics in order to suit agricultural necessities. Further, identifying and characterizing suitable priming agents (biotic or abiotic) and the host receptor sites for them will lead to successful implementation of this powerful biological tool in future. Seeds from primed plants when used for cultivation have the potentiality to put up a strong defence against the potential biotic and abiotic threats. Thus, strengthening the innate immunity of a plant through transgenerationally regulated phenomenon will help in significantly reducing synthetic pesticidal loads against the biotic challenges. Current understanding and future opportunities of induced transgenerational epigenetic changes in plants have led scientists to dream for a relatively pesticide-free environment which is also the need of the hour.

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Bhatnagar Laureates and Fellows of the Royal Society

I enjoyed the letter ‘Shanti Swarup Bhatnagar Prize: an inspiration for international recognitions’ by Singh and Luthra[1]. It is hardly surprising that there is such a strong correlation between winners of the Bhatnagar Award and Fellows of the Royal Society (FRS), as the Bhatnagar Award is one of the most prestigious awards in Indian science.

Table 1 in the letter lists only the Indian FRS who were elected after the institution of the Bhatnagar Prize. It would be useful to have a list of all Indian FRS. I believe that Srinivasa Ramanjuan was the very first Indian FRS.

There is at least one error in the table. Chandrashekhar B. Khare (UCLA) was elected as an FRS in 2012, along with K. VijayRaghavan and myself, but his name is missing from the list.

Finally, I would be curious to know whether there is any other instance of someone like me, who is an Indian citizen and an FRS, but received all of his university education abroad.

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Response:

We thank Vidyasagar for his appreciation of our letter. The table lists 39 scientists of Indian origin, who obtained their tertiary-level education from India and have been elected FRS since the institution of the Bhatnagar Award, and out of these 23 are Bhatnagar Awardees. The names of Vidyasagar and Khare, elected FRS in 2012, were not included as they have not obtained their tertiary-level education from India.

Ardaseer Cursetjee (Wadia) was the first Indian to be elected FRS in 1841 followed by Srinivasa Ramanujan in 1918 (ref. 1).

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