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Heterosis breeding in eggplant: A review

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Abstract
Heterosis (Or hybrid vigor) results in a hybrid's phenotypic superiority over its founder parents for quantitative and qualitative traits. Hybrid vigor is defined by mechanisms such as dominant complementation, over-dominance, and epistasis. Eggplant, originated from India, is the most important crop among solanaceous vegetables of the world. The improvement work was concentrated in several organizations with the objective to develop high yielding varieties which are resistant to biotic and abiotic stresses. During recent past, hybrids in vegetables have become very popular and bringing huge returns to the farmers. Considering the economic and nutritional significance of eggplant, breeding efforts focus on developing high-yielding varieties mostly F_1 hybrids with important traits. These hybrids have high yield potential, good adaptability resistance to biotic and abiotic stress and recommended for commercial cultivation in different agro-climatic conditions. Successful exploitation of heterosis in eggplant resulted in considerable improvement with respect to quantitative traits. In this direction, heterosis will be useful for developing most beneficial hybrid and hence a review on previous work in this line is presented.

Keywords: Eggplant, heterosis, quantitative traits

Introduction
Eggplant, popularly known as brinjal or aubergine (*Solanum melongena* L.) is important among the extensively cultivated vegetables. Consequently, it is also referred to as the common man's vegetable in the Indian subcontinent owing to its year-around availability (Saini *et al*. 2019) [45]. The cultivated area under eggplant cultivation is 1.79 million ha with a production of 51.28 million tons (FAOSTAT, 2019) [17]. Brinjal was one of the first vegetable crop in which hybrids were adopted by farmers. Hybrids, occupy more than 50% area in different parts of the country and is a significant source of income for approximately 14 lakh small and marginal farmers. In recent years, there has been increased preference among Indian farmers for cultivation of hybrid in vegetable crops. This has resulted in intense R&D activities by the Indian as well as multinational seed companies (Sidhu, 1998) [54]. Hybrid vegetables are well known in Japan, Netherland, USA and Canada, where the vegetable seed industry, in general, is well organized and highly developed, where more than 90% of the total eggplant seed are of hybrid origin. The productivity of eggplant in India is very low (17.2 t/ha) as compared to 41.2 tonnes in the France, where the F_1 hybrid constitute most of the economical cultivars. The required goals of increasing productivity in the quickest possible time can be achieved only through heterosis breeding which is feasible in this crop (kakizaki, 1931) [22]. Hence, the present review was under taken with an objective of highlighting the extent of heterosis in brinjal and then utilization in future crop improvement programmes.

Importance of heterosis breeding
Heterosis offer opportunities for improvement in productivity, earliness, uniformity, quality, wider adaptability and for rapid deployment of dominant genes for resistance to diseases and pests (Riggs, 1988) [44]. In vegetable crops, heterosis breeding has been found useful in the improvement of yield potential of self as well as cross-pollinated crops. Exploitation of heterosis for various characters has become a potential tool in the enhancement of brinjal (Singh *et al.* 1985) [56] (Shankaraiah and Rao, 1990) [52]. Bailey and Munson (1981) [6] were the first to conduct artificial hybridization in egg plant. The occurrence of hybrid vigour in egg plant has been reported by many workers. Hybridization is one of the means of exploitation of heterosis. It is an effective approach for yield and quality enhancement of vegetable crops. In order to identify superior hybrids for qualitative and quantitative aspects, it is essential to study

their mean performance along with combining ability and heterosis. Eggplant continues to be a choice of breeders for exploitation of heterosis due to hardy nature of crop, comparatively large size of flowers and large number of seeds in a single act of pollination. Highly varied consumer acceptance from region to region also demands for development of a large number of high yielding F_1 hybrids. Exploitation of hybrid vigor has become a potential tool for improvement in brinjal (Pal and Singh 1949, Mishra 1961, Samandam 1962, Dhankar *et al*. 1980, Chadha and Sidhu 1982) [35, 29, 46, 16, 11]. In India, several reports are available on hybrid vigor in brinjal. Pal and Singh (1949) [35] reported that brinjal brinjal showed 48.8-56.6% increased yields over the better parent. Mishra (1961) [29] also observed increased yields in brinjal hybrids. The cost of hybrid seed production is not high as compared to other vegetables and this can be further reduced by the use of male sterile lines.

Breeding objectives

Breeding activities in eggplant have been targeted at the development of high-yielding, early, better quality and disease resistant varieties. The color of the fruit and size and shape, the proportion of seeds to pulp, short cooking time and lower solanine levels are important traits in assessing quality. As brinjal is susceptible to several pests, and diseases such as wilt, *Phomopsis*, little leaf and root-knot nematodes and to insects such as shoot and fruit borer, jassids, epilachna beetle, etc. the development of multiple resistant varieties is a major challenges. Plants are susceptible to both low and high temperature; therefore attempts are being made to develop chilling or frost- tolerant and heat-tolerant varieties (Singh and Kumar, 2005; Senthilnathan *et al.*, 2018; Sarwary *et al.*, 2022) [55, 48, 49].

Specific breeding objectives in eggplant in Indian context are

a) Exploitation of heterosis for increasing productivity
b) Incorporation of resistance against insect pests including fruit and shoot borer
c) Breeding for wilt and other disease resistance
d) Development of cultivars with better quality
e) Improvement of locally preferred cultivars which are distinct

Exploitation of heterosis

The term heterosis was coined by Shull in 1914. Heterosis refers the superiority of F_1 in one or more characters over its parents obtained by crossing two genetically dissimilar individuals. Generally, the term hybrid vigor is used to denote heterosis in the dissimilar direction and the heterosis over mid parent, better parent and standard check (ruling variety/hybrids) is designated as heterosis, heterobeltiosis and standard heterosis respectively.

The phenomenon of heterosis or hybrid vigour is well known today and breeders exploit it for higher production. The earliest recorded instances of artificial hybridization in eggplant were evidently those carried out by Bailey and Munson in the United States in 1889, however none of the hybrids exhibited heterosis but were intermediate between the parents (Bailey and Munson, 1892) [4]. The first positive report of heterosis in the eggplant came from Munson (1892) [4]. Subsequently, Halsted (1901) [18] reported that in one of the crosses fruit were was double the size of the parental line and also yielded more. In the Philippines, Bayla (1918) [7] hybridized some local varieties and found that the hybrids were more vigorous, stronger and healthier than the respective parental lines. In Japan, Nagai and Kida (1926) studied certain quantitative characteristics in the hybrids and found that heterosis was manifested in total yield and its traits. Tatesi (1927) [58] observed higher productivity in certain crosses between Japanese brinjal varieties. Kakizaki (1928) reported the occurrence of remarkable hybrid vigour in the crosses with regard to seed weight, stem diameter and height in brinjal. Schmidt (1935) [47] in USSR observed that the character of earliness was dominant and even transgressive in certain eggplant crosses. Daskaloff (1941) [14] indicated the possibility of utilization of heterosis in commercial eggplant production in Germany.

Averjanova (1941) [3] from Bulgaria reported high yields from hybrid eggplants. Odland and Noll (1948) [34] experimented with sixteen hybrid types and recorded that in every case the hybrids out yielded their respective parents besides being early. Capinpin and Alviar (1949) [10] reported that hybrid seeds exhibited higher germination percentage, the hybrid plants were superior to the parental lines in early flowering and setting of fruit, greater number of fruits per plant, longer fruit, greater mean of equatorial diameter of the fruits and greater mean weight of the fruits, Daskalov (1955) [15] from Bulgaria reported high yields from hybrid eggplants.

In India the first attempt to hybridize eggplant appears to have been made by Rao in 1934 [42], however, in the cross between two wide varieties, a high degree of partial sterility due to abortive pollen was observed. Venkataramani (1946) [61] reported that hybrid egg plants were taller, spread more, flowered earlier than the early parent and yielded more than either parent. In the same year, Pal and Singh (1946) [36] reported that majority of the hybrids exhibited heterosis with respect to seed germination, plant height, plant spread, number of branches, early flowering, number of fruits per plant, fruit size and fruit yield.

Plant height

Rajaneesh and Maurya (2005) [40] found heterosis for this trait in the cross Type 3 x Ramnagar Giant over better parent (55.00%) and Type 3 x Pant Samarat over mid parent (56.04%). Vaddoria *et al.* (2007) [59] reported the heterosis percentage in the cross JBCL 01-1 x PLR 1 over mid, better and standard parent (33.02, 28.67, 6.50%) respectively. Suneetha *et al.* (20081) [57] reported the heterobeltiosis in the cross Morvi 4-2 x SR (42.76%) and standard heterosis in BG x SR (23.38%). Ansari *et al.* (2009) [2] reported the heterosis in the cross Chianki Local-1 x Chianki Local-2 (36.11%) over mid parent and CH-894 x Chinaki Local-1 (23.11%) over better parent. Hazra *et al.* (2010) [19] reported the relative heterosis in the cross Uttara x Nawabganj Local (52.45%) and the heterobeltiosis in Uttara x Nawabganj Local (35.58%). Ramesh *et al*. (2013) [41] reported that the cross Sedapatty x Annamalai recorded heterosis of 44.42, 29.76 and 71.03% over mid, better and standard parent respectively.

Raghvendra *et al.* (2014) [39] reported that the heterobeltiosis was recorded in Sel-5 x PPC (32.35%). Venkatanaresh *et al.* (2014) [60] found better parent heterosis of 26.28%in the cross KS-6103 x KS-8821. Vidhya (2015) [62] found heterosis for plant height in the cross 1S x IC 354721 (29.08%) over mid parent, CO 2 x HD 2 (26.27%) over better parent and 1S x IC 354721 (45.46%) over standard heterosis. Mistry *et al.* (2018)

[30] reported heterosis in the cross Doli-5 × GBL-1 (12.8%) over mid parent and (19.12%) over better parent.

Number of branches per plant

Rajaneesh and Maurya (2005) [40] reported that the cross KS 352 x Pant Samarat recorded the heterosis over better parent (98.66%) and mid parent (63.28%). Shafeeq *et al.* (2007) [50] reported that the extent of heterosis exhibited by the F_1s over their corresponding better parent ranged from -40.68% (Arka Sheel x Kudachi A) to 22.76% (Arka Nidhi x Green Round). Bhakta *et al.* (2009a) [8] reported that the hybrid AB 03-3 x GOB-1 recorded the heterobeltiosis (34.66). Abhinav and Mehta (2010) [1] reported that the cross IGBO 83 x BB 93 (41.69%) recorded the heterosis over better parent.

Bhushan and Singh (2013) [9] reported the heterosis in the cross PB 68 x PS over relative heterosis (18.85%) and BARI x PS (27.77%) over standard heterosis. Ramesh *et al.* (2013) [41] reported that the cross Melur Local x KKM 1 recorded 50.67% over mid parent and 18.01% over standard check and Palamedu Local x KKM 1 (35.19%) over heterobeltiosis. Reddy and Patel (2014a) [43] that the standard heterosis was recorded in AB 8 /5 x GJB 2 (23.74%). According to Vidhya (2015) [62], the cross IC 354721 x HD 1 recorded 55.0% over mid parent and better parent heterosis for this trait. Mistry *et al.* (2018) [30] recorded that the hybrid Doli-5 × GBL-1 (120.3%) over mid parent and Doli-5 × KS-331 (107.5%) have registered higher significant positive over better parent values.

Days to first flowering

The negative heterosis for days to first flowering was observed as -14.08, -15.48 and -15.8% over mid, better and standard parent respectively in the cross Nilakottai Local x Annamalai (Kumar *et al.* 2013) [26]. Reddy and Patel (2014a) [43] recorded the negative standard heterosis in AB 7 / 2 x GJB 2 as -29.44%. According to Shahjahan *et al.* (2016) [51] the significant negative better parent response for earliness (-12.08%) was found in cross Ral 3 x BARI Begun 7. Mistry *et al.* (2018) [30] stated that the hybrids Doli-5 × KS-331 (-1.48%) and Doli-5 × KS-331 (-2.37%) have recorded negative heterosis over better and mid parent respectively for days to first flowering.

Days to 50 percent flowering

Shafeeq *et al.* (2007) [50] reported the heterosis over mid parent ranged from -7.87% (Arka Shirish x Malapur Local) to -28.08% (Arka Nidhi x Malapur Local). The extent of heterosis percent ranged from 10.34% (Arka Shirish x Kudachi B) to -19.78% (Arka Nidhi x Malapur Local). Vaddoria *et al.* (2007) [59] recorded -7.42% as in the cross DBL 21 x PLR 1 over better parent. Chowdhury *et al.* (2010) [13] reported negative heterosis over better parent -27.59% in the hybrid Volanath x Nayantara. Bhushan and Singh (2013) reported negative heterosis in the cross PB 64 x PU over relative heterosis (-23.53%), heterobeltiosis (-21.43%) and (-23.93%) over standard heterosis.

Jay *et al.* (2013a) reported negative heterobeltiosis in PR x PB (-11.0%). Raghvendra *et al.* (2014) [39] reported negative heterobeltiosis in FB-18 x Pant Samrat (-12.5%). Reddy and Patel (2014a) recorded negative standard heterosis in AB 7 / 2 x GJB 2 (-22.51%). Venkatanaresh *et al.* (2014) [60] observed better parent heterosis of -23.08% in the cross KS-6103 x KS-8821. Vidhya (2015) [62] reported negative heterosis in the cross 1S x CO 2 (-7.52%) over mid parent and CO 2 x HD 2 (-11.06%) over heterobeltiosis and HD 1 x HD 2 (-13.94%).

Days to first harvest

Voddoria *et al.* (2007) [59] reported that the hybrid DBL 21 x PLR 1 was promising over BP, MP and standard parent. Ansari *et al.* (2009) [2] reported negative heterosis in the cross CH-885 x Chianki Local-2 (-12.7%) over mid parent and -21.94% over better parent. Bhakta *et al.* (2009a) [8] reported that the hybrid ABR 02-23 x Surti Ravaiya (-16.95%) exhibited the negative heterobeltiosis followed by GOB-1 x Surti Ravaiya (-9.60%) and AB 03-13 x GOB-1 (-8.60%). Makani *et al.* (2013) [28] reported relative heterosis over mid parent in Pusa Uttam x AB-07-08 (-14.71%), better parent in PPL-1 x Pusa Uttam (-12.64%) and standard heterosis in GBL-1 x KS-331 (-4.44%). Venkatanaresh *et al.* (2014) [60] reported that the cross KS-6103 x KS-8821 exhibited better parent heterosis of -21.21%. Mistry *et al.* (2018) [30] reported negative heterosis in the cross AB 07-02 × GOB 1 (-0.56%) over mid parent and the cross Doli-5 × GBL-1 (-1.53%) over better parent.

Fruit length

Rajaneesh and Maurya (2005) [40] reported that the cross JB 15 x Ramnagar Giant recorded the heterosis over better parent (39.31%) and mid parent (79.12%). Kamal *et al.* (2006) [23] found the heterosis for this trait in the cross Pant Rituraj x KS 227 (25.52%). Prakash *et al.* (2008) [38] reported that the magnitude of standard heterosis in DWD-8 x DWD-9 (10.66%). Abhinav and Mehta (2010) reported that the cross IGBL 67 x BB 93 (13.55%) recorded the heterosis over better parent. Kuldeep *et al.* (2012) [24] reported that the cross BR-112 x Aruna (56.67%) recorded the heterosis over better parent. Bhushan and Singh (2013) [9] reported the heterosis in the cross PB 68 x PU over relative heterosis (76.8%), heterobeltiosis (23.66%) and (73.04%) over standard heterosis.

Venkatanaresh *et al.* (2014) [60] recorded better parent heterosis of 70.51%in the cross KS-5623 x KS-7512. Vidhya (2015) [62] reported that the cross HD 1 x IC 354721 recorded better parent heterosis of 35.69%. According to Kumar *et al.* (2017) [25] the heterosis for fruit length varied from - 41.85 (PLR-1 X Doli-5) to 9.28% (PLR-1 X GOB-1) greater than Surati Ravaiya and -46.58 (PLR-1 X Doli-5) to 0.39% (PLR-1 X GOB-1). Mistry *et al.* (2018) [30] reported the heterosis which ranged from 15.08 to 47.08%and 6.12 to 40.49%over mid and better parent, respectively. The economic heterosis to the extent of 47.08%was recorded in a cross combination of AB 07-02 × GOB.

Fruit girth

Prabhu (2004) [37] noted relative heterosis in EP 104 x APAU Bagmathi (8.44%) and heterobeltiosis (2.95%) and standard heterosis (4.67%) in the cross MDU 1 x Surya. Rajaneesh and Maurya (2005) [40] reported that the cross Type 3 x Pant Rituraj (12.90) recorded the heteroisis over better parent and Aruna x Pant Samarat (17.68) recorded the heterosis over mid parent for this trait. Kamal *et al.* (2006) [23] reported that the cross Pant Rituraj x KS-227 (29.72%) recorded the heterosis. Abhinav and Mehta (2010) [1] reported that the cross IGBL 70 x IVBL 9 (50.96%) recorded the heterosis over better parent. Chowdhury *et al.* (2010) [13] recorded the heterosis over better parent in the hybrid BARI Begun-8 x Volanath (24.14%).

Makani *et al.* (2013) [28] reported heterosis in GP-180 x KS-331 over mid parent (34.58%), better parent (28.83%) and standard check (26.05%).
According to Kumar *et al.* (2017) [25] the standard heterosis varied from -19.09 (KS-224 x GOB-1) to 68.70% (GJB-3 X GBL-1) more than Surati ravaiya and -25.83% (KS-224 X GOB-1) to 54.64% (GJB-3 X GBL-1) more than GBH-2. Mistry *et al.* (2018) [30] observed significant and positive heterosis over mid parent, and it ranged from 8.30% in Doli-5 × GBL-1 to 19.15% in AB 07-02 × GOB 1.

Single fruit weight

Shafeeq *et al.* (2007) [50] obtained heterosis over mid parent in Budihal Local x Kudachi A (96.3%) and 69.22% over better parent. Prakash *et al.* (2008) [38] reported that the magnitude of heterosis was in DWD-8 x DWD 1 (52.90%) over better parent and DWD-8 x DWD-2 (180.63%) over standard check. Ansari *et al.* (2009) [2] reported heterosis in the cross Chianki Local-1 x Chianki Local-2 (95.58%) over mid parent and 79.70% over better parent.
Hazra *et al.* (2010) [19] observed the relative heterosis in PPC x Pusa Anupam (40.42%) over mid parent and HE 12 x Singnath (41.03%) over better parent. Nalini *et al.* (2011) [33] reported that the extent of heterosis over Local check was with 26.33% in the cross MG x IC-909. Kuldeep *et al.* (2012) [24] reported that the cross H-7 x Pb Neelam (35.99%) recorded the heterosis over better parent. Jay *et al.* (2013a) reported heterobeltiosis in PR-5 x RCMBL-1 (186.34%). Raghvendra *et al.* (2014) [39] reported heterobeltiosis in FB-18 x Pant Samrat (48.42%). Reddy and Patel (2014a) [43] recorded standard heterosis in JBR 6/7 x GJB 2 (17.53%). Venkatanaresh *et al.* (2014) [60] recorded better parent heterosis (19.25%) in the cross KS-7570 x KS-8821. Mistry *et al.* (2018) [30] reported highly significant positive heterosis over better parent in the cross Doli-5 × KS-331 (19.80%).

Number of fruits per plant

Prabhu (2004) recorded heterosis in EP 65 x Pusa Uttam) over mid parent (52.82%) and better parent (42.37%). Kamal *et al.* (2006) [23] reported the heterosis of 64.84% in the hybrid Pant Rituraj x JB 64-1-2 expressed. Shafeeq *et al.* (2007) [25] reported heterosis over mid parent in Arka Nidhi x Green Round (22.91%) and heterobeltiosis in Budihal Local x Kudachi A (43.62%). Prakash *et al.* (2008) [38] recorded heterobeltiosis in DWD-15 x DWD-2 (30.64%). Bhakta *et al.* (2009a) [8] reported that the hybrid AB 03-3 x GOB-1 exhibited significant positive heterosis over better parent (20.11%). Chowdhury *et al.* (2010) [13] recorded the of 105.00% (Nayantara x Khatkhatia) and 253.65% (Kazla x Khatkhatia) heterosis recorded over better parent and standard check respectively.
Makani *et al.* (2013) [28] reported heterosis in NDB-18 x GP-180 over mid parent (168.45%), PPL-1 x GP-180 over better parent (190.34%) and GBL-1 x KS-331 over standard check (65.11%). Venkatanaresh *et al.* (2014) [60] found better parent heterosis (67.0%) in the cross KS-5623 x KS-7512. Vidhya (2015) [62] reported the heterosis was recorded by the cross HD 2 x CO 2 (27.80%) over mid parent, IC 354721 x 1S over better parent and HD 1 x HD 2 (8.05%) over standard heterosis. Mistry *et al.* (2018) [30] recorded 30.48 and 28.50% (AB 07-02 × GOB 1) heterosis in the cross (AB 07-02 × GOB 1) over mid and better parent respectively.

Fruit yield per plant

Chaudhary, (2006) [12] reported that the extent of heterosis varied from -26.06 (PPC x SM 6-7) to 64.08% (Punjab Barsati x SM 6-7) over better parent and standard check. Prakash *et al.* (2008) [38] reported that the magnitude of heterosis was in DWD-15 x DWD-9 (50.66%) and DWD-15 x DWD-9 (27.74%) over better parent and standard check respectively. Bhakta *et al.* (2009a) [8] reported that the hybrids AB 03-3 x GOB-1 (26.86) and GOB-1 x Surati Ravaiya (26.60) exhibited significant positive heterobeltiosis.
Hazra *et al.* (2010) [19] recorded that heterosis percentage of 107.35% in Uttara x Nawabganj Local over mid parent and 83.08% in Uttara x Pusa Anupam over better parent. Nalini *et al.* (2011) [33] reported that the hybrid IC-112 x IC-996 exhibited the heterosis of 72.7% over Local check. Kuldeep *et al.* (2012) [24] reported that the cross H-9 x S-16 recorded the heterosis (39.52%) over better parent. Ramesh *et al.* (2013) [41] found heterosis of 75.36, 59.03 and 34.07% over mid, better and standard parent respectively in the cross Keerikai Local x KKM 1. Venkatanaresh *et al.* (2014) [60] found better parent heterosis of 111.84% in the cross KS-8507 x KS-7512. Vidhya (2015) [62] found heterosis in the cross IC 354721 x HD 1 (6.93%) over mid parent and CO 2 x HD 1 (4.61%) over standard heterosis for this trait.

Conclusions and Future Perspective

Heterosis is regarded as a result of genome interactions, leading in complex modifications at genetic, epigenetic, biochemical, and regulatory network levels. In recent decades, several efforts have been performed in heterosis related research. In the field of heterosis research, new technological advancements have facilitated a better understanding of the heterosis phenomena. Therefore, most of the studies involving crossing in eggplant end up in the estimation of the extent of heterosis. Although eggplant has undergone an enormous selection pressure for the trait especially higher yield. Moreover, even when developing hybrids for disease and insect pest resistance yield is generally not compromised.
Furthermore, to keep with growing market demand of eggplants, the hybrids are desired by the farmers because of their higher yield potential. But the hybrid performance depends on the parents (Inbreds) used in the hybridization program. Generally, distinct inbreds lead to more heterotic hybrids. Whereas in eggplant, this may vary as in a recent study, it was pointed out that SNPs based genetic distance determined for the morphological and the biochemical traits does not significantly affect the heterosis in eggplant. Heterosis exploitation is significant in eggplant to obtain traits like higher vitality, better growth and development, insect and pest resistance and uniformity. With a relatively less cost of hybrid seed production in eggplant and the availability of male-sterility mechanism, the development of new hybrids is straight forward. In this context, a significant challenge is to accurately track and quantification of the diverse heterotic phenotypes that contribute to nearly all heterotic traits.

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