



REVIEW ARTICLE

Unravelling the trait genetics in cool season legumes using generation mean analysis

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Abstract

Generation mean analysis (GMA) is a biometrical technique in plant breeding, used to elucidate the non-allelic interactions (NAI) associated with polygenic traits. The GMA utilises a maximum of 6 generations of a cross: P_1 and P_2 (parents), F_1 and F_2 (first and second filial generations) and BC_1 and BC_2 (back cross). The GMA is a two-step process: Estimation of, (i) epistatic interaction using a scaling test and (ii) effects of genetic components. Such dissection helps a breeder to select optimal plant breeding methods for improving the crop of interest. Cool-season legumes (CSL) owe macro and micronutrient richness and thereby assume nutritional significance. The CSL warrant genetic improvements to feed the rapidly growing global population. The role of classical hybridisation techniques is particularly important. To harness the improvement, a compiled genetic information on CSL is highly essential, which is yet to be published. Therefore, this review compiles the botanical introduction, nutritional significance and breeding behaviour of CSL. In addition, the genetic studies involving the GMA in CSL from 2012 to 2025 are compiled. Many GMA studies were published in major CSL like chickpeas and in the underutilised but potential legumes like horse gram it is yet to be published. From the GMA, it is inferred that (i) the six-parameter model with combined scaling (individual and joint scale) test is predominantly utilised and (ii) both additive and non-additive gene effects govern many of the yield and its contributing traits. However, non-additive effects (dominant gene) showed high magnitude with duplicate epistatic gene interaction suggesting utilisation of biparental hybridisation or recurrent selection for improvement.

Keywords: cool-season legumes; generation mean analysis; gene interaction; parameter models

Introduction

The word legume (derived from the Latin Legumen) refers to all plants belonging to the family Fabaceae comprising 753 genera and 20000 species. "Pulses" are a subset of "legume," particularly those grown and harvested for their dry edible seeds and usually called grain legume. Generally, legumes are rich in protein (20–45 %) and consist of essential amino acids, fibre, vitamins and minerals (1). Legumes in association with rhizobium fixes atmospheric nitrogen in the soil as ammonia, which improves the soil fertility and reduce the requirement of synthetic fertilisers (2). In a multiple and intensive cropping system, legume cultivation creates a synergistic effect on the subsequent crops through increased yield (3). Cool-season legumes are significantly contributing to human and animal nutritional security (4). They are widely distributed geographically but generally grown in temperate and subtropical environments. The grains of chickpea, lentil, pea and broad beans are cool-season legumes known for their nutritional potential and serve as the best alternate to animal protein (5). A biometrical method is always

helpful to plant breeders to estimate the genetic governance of traits. The generation mean analysis (GMA) is a simple yet useful biometrical technique used for characterising the non-allelic interactions in polygenic characters. This estimation is considered important because polygenic traits are controlled by many loci, which express different degrees of dominance and direction of gene action. Interactions between these loci are commonly observed and they may be of additive x additive, dominance x dominance and additive x dominance types. The GMA analysis is based on 6 basic generations or populations, P_1 , P_2 , F_1 , F_2 , BC_1 and BC_2 , where P_1 and P_2 are diverse parents (which may be an inbred, homozygous or true breeding lines (TBLs)). F_1 is a hybrid produced by crossing P_1 and P_2 . The F_2 is the segregating generation produced by selfing F_1 . BC_1 is the first backcross generation involving F_1 and P_1 . BC_2 is the second backcross generation ($F_1 \times P_2$). Mean values of these generations of a cross are used to estimate the genetic components of variation and gene effects. The analysis consists of two steps, viz., (i) testing for epistatic interaction and (ii) estimation of genetic

components and gene effects. From these results, a breeder can choose appropriate breeding methods to improve the trait of interest. A compiled GMA review is yet to be published in the cool-season legumes (CSL), therefore, this paper addresses such a gap.

The procedure of the GMA comprises the following steps,

A. Scaling tests (ST)

The scaling tests (Mather, 1949), in the plant breeding experiments, detect the presence of epistasis (non-allelic interaction (NAI)) in the polygenic traits. Mather utilised three scales (A, B and C) to test the NAI from the datasets of four generations viz., P_1 , P_2 , F_1 and F_2 . From the results of the scaling test (ST), the methods of estimation of genetic components are inferred. The ST is working on the assumptions like autosomal inheritance, absence of maternal inheritance and absence of differential fertility and viability. In 1955, Hayman added a fourth scaling test (D scale) with the Mather model. The results of the ST are inferred as follows: (i) if the values of all 4 scales are zero: No epistasis and the additive-dominance model is fit, (ii) if the value is significantly different from zero: epistasis is present and the additive-dominance model is not adequate. Significance for any of the scales based on the t -test

indicates the presence of epistatic interaction. Based on the presence or absence of epistasis (revealed from scaling tests), different models are used to estimate the gene effects. The ST is illustrated in Fig. 1 for a comprehension. It illustrates the scales used the scaling test and the inferences drawn from the scaling tests. A few drawbacks of the ST are (i) from the 6 populations, only three or four are considered for testing at a time; (ii) it does not provide estimates of mean effects (m), additive effects (d) and dominance effects (h); and (iii) it does not test the goodness of fit of a model. To overcome these drawbacks, Cavalli in 1952 devised a joint scaling test (JST), based on 4 generations. It includes the estimation of (m), (d) and (h) and checks the significance of the chi-square test between observed and expected means of different generations. The significance of the chi-square test indicates the presence of epistasis. The JST is illustrated in Fig. 2 for an easy understanding. It illustrates the metrics arrived from the JST and their inferences. The estimates of m , d , h , i , j and l indicate the average performance of a trait over generations, heritable portion of the total variation, heterotic effect in a locus, homozygous interaction effects, interaction between dominant alleles of different loci, the effect of homozygous of a locus with dominant allele of another locus

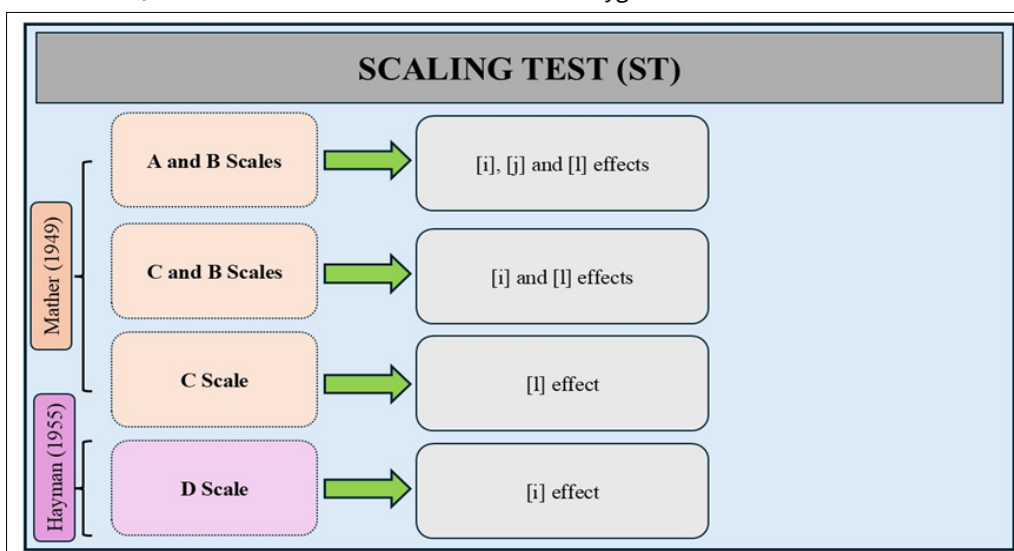


Fig. 1. Scaling test (ST).

[i]: additive $\times$ additive effect; [j]: additive $\times$ dominance effect; [l] dominance $\times$ dominance effect.

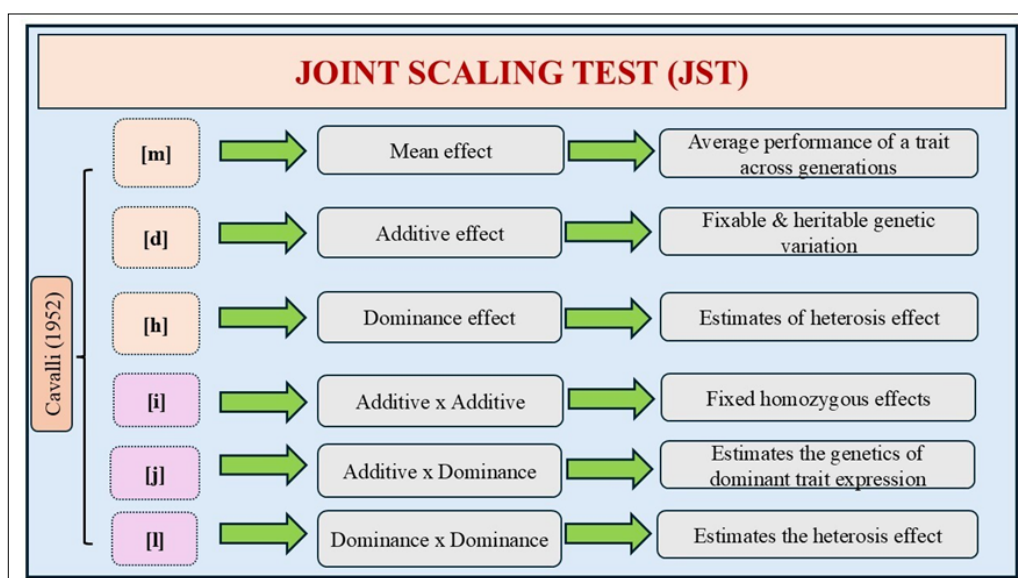


Fig. 2. Components of the joint scaling test.

[m]: mean effect; [d]: additive effect; [h]: dominance effect.

respectively. When scales A, B and C are non-significant in the JST, it infers that epistasis is absent and additive-dominance components can explain the total variability. In this case, the three-parameter model can be used to estimate three genetic components, viz., m , d and h . When gene interaction is absent, m is the mean residual effect; while d and h are additive and dominance effects respectively. In the presence of epistasis, the six or five-parameter model can be utilised to estimate the interaction effects.

B. Estimation of genetic effects

Three types of GMA models: three, five and six-parameters can be used to estimate the genetic effects. A parameter is defined as a numerical quantity which describes some characteristics of a population. The three-parameter model (TPM) is used in the absence of non-allelic interaction. The TPM estimates m , d and h . In the five-parameter model (FPM), genetic components m , d and h and the effects of two epistatic interactions, additive $\times$ additive (i) and dominance $\times$ dominance (l), are estimated. For this analysis, the means of P_1 , P_2 , F_1 , F_2 and F_3 generations are used. In the FPM, the role of inter-allelic interactions is not estimated effectively despite their major role in gene expression. To overcome this, Hayman, Jinks and Jones in 1958 developed the six-parameter model (SPM) for the estimation of various components of genetic variance. The SPM can deduce the apparent contributions of non-allelic interactions. Also, it estimates gene interactions, additive $\times$ additive (i), additive $\times$ dominance (j) and dominance $\times$ dominance (l). The SPM uses means of 6 generations. The pictorial representation of GMA models is represented in Fig. 3. It illustrates the different GMA models and the required generations. The TPM utilises 6 generations (P_1 , P_2 , F_1 , F_2 , BC_1 and BC_2), FPM utilises P_1 , P_2 , F_1 , F_2 , F_3 or BC_1 and SPM uses P_1 , P_2 , F_1 , F_2 , BC_1 and BC_2 . The TPM does not estimate epistasis, FPM analysis specific epistasis types, SMP estimates all types of epistatic interactions.

Cool season legumes

Chickpea (*Cicer arietinum* L.)

Botanical background: It is a diploid CSL ($2n = 16$) with a genome size of 738.09 mb (6). The name “chickpea” is attributed to the seed shape, which resembles a chicken's head with a beak. It originated from Western Asia (Turkey)/ Southwestern Asia (Afghanistan). Chickpea is a spreading or erect annual and branching species. The

chickpea leaves are sour due to malic (90–96 %) and oxalic acid (4–10 %). The flowers are pink to white coloured. The pods contain 1–3 beans with a little hilum at the front end and a noticeable beak at the anterior end. Based on seed traits chickpea is classified as (i) desi type (*Cicer arietinum* L.); small-sized, light and dark, brown-coloured seeds with a thick seed coat and (ii) Kabuli type or garbanzo beans, large seeds with a pale cream-testa. Chickpea matures in 90–115 days.

Cultivation requirements: Chickpea is well-suited to arid and semi-arid regions and requires an optimal temperature of 24–30 °C. It is susceptible to frost, waterlogging, saline and alkaline conditions.

Nutritional significance: Dried chickpeas contain 19.3–21 % protein, 5.3–6.0 % fat and 62 % carbohydrates. Tryptophan, valine, threonine and sulphur amino acids are the primary limiting amino acids (7). The palmitic acid, stearic acid and unsaturated fatty acids (oleic, linoleic and linolenic acids) is the fatty composition. It is considered a nutritious and healthy food because of its high dietary fibre (17.4 %), low-fat and extremely low glycemic index (28 %). It has blood purification ability. Sprouted beans are rich in vitamin C.

Breeding behaviour and genetic improvement through GMA: Chickpea is a self-pollinated crop; the classical breeding techniques like introduction, hybridisation, simple backcrosses, three-way crosses, multiple crosses, pedigree method, bulk method and single seed descend (SSD) method are employed for its improvement (8). The targeted traits for improvement are growth habit, leaf type, tall-erect cultivars, pod size, shape and hue, maturity duration and extra-large seeded in Kabuli type, dehulling percentage, pod dehiscence, resistance to root rot (dry), grey mould, ascochyta blight, wilt (fusarium), tolerance to stress environments like cold, heat (reproductive stage), drought, saline and alkaline soils, resistance to pod borer, improved water and nutrient use efficiency, enhanced zinc (Zn) (more than 40 ppm), iron (Fe) (more than 60 ppm) and protein (more than 25 %) contents, increased seed yield and biomass, increased photosynthetic rate, enhanced chlorophyll content, root characteristics, water-soluble carbohydrates and mechanical harvestable varieties (9). Various breeding efforts have been undertaken to improve these traits. Of them, the genetic information arrived after GMA are compiled and presented for a comprehensive understanding (Supplementary Table 1) (10–23).

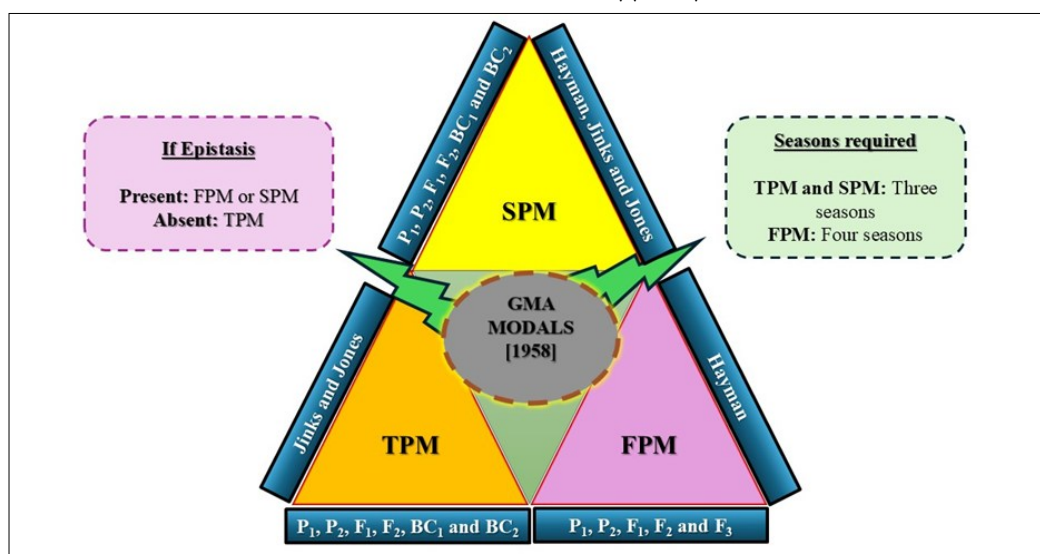


Fig. 3. Details of the generation mean analysis (GMA) models.

TPM: three parameter model; FPM: five parameter model; SPM: six-parameter model.

Common bean/kidney bean/French bean/garden bean/faraz bean/ dwarf bean/haricot bean (*Phaseolus vulgaris* L.)

Botanical background: It is originated from Mexico. It is a diploid CSL and the genome size is 587 mb (24). The four primary types are kidney, navy, cranberry and black turtle beans. It is a low, erect or twining, determinate annuals with small white coloured flowers and has slender pods. It has the characteristic spirally twisted keel. The bean has a white hilum and kidney-shaped, oblong, or globular. It is a shy nodulator.

Cultivation requirements: French bean is a day-neutral crop and it is most sensitive to salt and sodicity.

Nutritional significance: It has 22 % protein, 1.6 % fats, 57.8 % carbohydrates, 4 % fibre and is a rich source of Fe, phosphorous (P) and vitamin B₁.

Breeding behaviour and genetic improvement through GMA: It is a typical self-pollinated crop. The classical crop improvement techniques like pedigree breeding, backcross, recurrent selection and single pod descent (SPD) method are employed for its improvement (25). The targeted traits for improvement are a short growing period, determinate growth habit, high quantity of pods per plant and enhanced grain weight, resistance to common bacterial blight (CBB) disease and angular leaf spot. Additionally, the goal includes improved protein content, low lipid content, high mineral content as well as desirable seed shape (26, 27). Many plant breeding attempts are made to improve the above-listed traits, including the GMA. The exclusive compiled information on these studies is presented in Supplementary Table 2 (28–32).

Pea (*Pisum sativum* L.)

Botanical background: It originates from mediterranean region. It is a diploid autogamous and the genome size is 4.45 Gb (33). It is an annual climber; possess a thin, hollow stem and inflated pods with 2–10 seeds. It is classified by several ways: (i) based on its vegetative growth (bush/vine types; tall/dwarf types), (ii) harvesting time (early, mid-season or late main season crop), (iii) seed colour (yellow cotyledons and green cotyledons) and (iv) seed texture (smooth-round seeded or wrinkle-seeded). The pea seeds lack endosperm. Peas were originally only eaten as a dry pulse. It wasn't until the 16th century that green peas were eaten.

Cultivation requirements: Field pea performs well in a mild cool season with fair rainfall.

Nutritional significance: The dried mature seeds have 22.5 % protein, 1 % fat, 62 % carbohydrates and 4.4 % fibre (34, 35). Peas have a lower glycaemic index, fewer allergens and are gluten-free (36). Pea lectin possesses cancer-fighting properties (37).

Breeding behaviour and genetic improvement through GMA: It is a strict autogamous species and therefore, the classical hybridisation procedures are extensively utilised to develop newer varieties. The targeted traits for improvement are earliness, plant stature, green seed varieties, pod length, number of nodes to the first flower, tolerant/ resistance to biotic (powdery mildew, rust, fusarium root wilt/rot and stem fly) and abiotic (high temperature tolerance, drought and salinity) stresses, lodging resistance, enhancement of nutritional content, reduction of anti-nutritional factors like low raffinose family oligosaccharides (RFO) content, pods count per plant, higher seed count per pod, higher biomass and high yield (38). The GMA was adequately utilised to learn the genetic control of several of the above-mentioned characters (Supplementary Table 3) (39–45).

Broad bean (*Vicia faba* L.)

Botanical background: Broad bean is an ancient legume, also known as the Windsor bean, fava bean, bakla bean, winter bean and faba bean. It is often grown as a cover crop. Its diploid chromosome number is 12 with a genome size of 13 Gb. The plant is a strong, erect annual with flat pods and large seeds. Based on its seed size, four distinct groups are categorised (i) major (largest seed size; broad bean), (ii) equine (medium size; field or horse bean), (iii) minor and (iv) paucijuga.

Cultivation requirements: It requires cool and temperate/subtropical climate. Optimal temperature requirement range is from 18–24 °C. It requires sufficient moisture for flowering and podding.

Nutritional significance: The protein content of broad beans varies from 26–30 %. The seeds and young pods are eaten as a vegetable. It has rich complex carbohydrates, choline, dietary fibre, lecithin, secondary metabolites (phenolic compounds) and minerals (46). Also, it has low fats, low sodium and is cholesterol-free (47).

Breeding behaviour and genetic improvement through GMA: It is a self-pollinated crop where classical hybridisation techniques like pedigree breeding, backcross, recurrent selection (RS) and SSD are employed for its improvement (48). The most important targeted traits for improvement are flower duration, plant height, growth habit, improving the nodule formation, stem count, maturity, chocolate spot resistance, rust resistance, pods count per plant, hundred seed weight, pod length, pod yield per plant, harvest index and total biomass yield (49–51). Genetic experiments were undertaken to infer the breeding behaviour of the traits using GMA and the inferences are compiled and presented in Supplementary Table 4 (52–63).

Lentil (*Lens esculenta* Moench.)

Botanical background: It is genetically a diploid CSL (2n = 14). It is originated in the Mediterranean and Southwest Asia. The genome size is about 4–4.3 Gb. It is one of the early domesticated legume crops. It was a common food of the ancient Greeks, Jews, Egyptians and Romans. Lentil greatly resembles chickpea in habit. It is a twining, slender tufted branched annual herb with a slender, angular stem. The leaves are pinnate and flowers are borne singly or in clusters of two or three at the tips of flowering branches. The pods are short and broad and contain only two lens-shaped seeds, which give the plant its name *Lens*. In the Indian trade, two types of lentils are commonly recognised: the bold-seeded form known as *Masur* or *Malka Masur* and the small-seeded known as *Musri*.

However, in the world trade, it is classified as macro and microsperma. Microsperma type: It has small, rounded seeds, 2–6 mm diameter, yellow or red-orange cotyledons and pale yellow to black testa. Predominantly grown in India, Nepal, Bangladesh, Pakistan, Afghanistan, Ethiopia and Egypt. Macrosperma type: It has large-size flattened seeds (6–9 mm diameter), yellow cotyledons with pale-green testa. Commonly cultivated in the Mediterranean, Spain, Italy, Greece and North and Latin America. Lentils have the highest nitrogen-fixing capacity among pulses. Generally, the lentil matures in three and a half months.

Cultivation requirements: Lentil requires a well-drained and sandy soil. It needs cooler temperature during vegetative growth and warmer temperature at maturity. The optimal temperature range is from 18–30 °C. It tolerates frost.

Nutritional significance: The protein content is 24–26 %. It is a rich source of vitamin B₂ and C and minerals (K, P, Ca, Fe and Zn) and it also contains significant amounts of oleic, linoleic and palmitic acids (64, 65). Amongst plant-based foods, lentils contain high levels of folate as well as beta-glucans, making their glycaemic index exceptionally low and suitable for wide health benefits. The presence of phytochemicals such as phenolic acids, flavanols, saponins, phytic acid and condensed tannins makes lentils rich in antioxidant properties (66).

Breeding behaviour and genetic improvement through GMA: Lentil is a self-pollinated crop. The breeding methods common for self-pollinated crops, viz., pure line selection, pedigree method and back cross methods are all followed by lentil breeders. The most important targeted traits for improvement are early maturity, uniform seed size, stress tolerance (heat, salinity and drought), quick cooking time and improving pod yield. Genetic experiments were undertaken to infer the breeding behaviour of the traits using GMA and the inferences are compiled and presented in Supplementary Table 5 (67, 68).

Conclusion

The cool season legumes (CSL) are assuming importance in food, fodder and eco-friendly cultivation perspectives. Genetic improvement of CSL is required to cater to the global food and fodder requirements. The biometrical technique generation mean analysis (GMA) is widely employed in only a few CSL to understand the genetic architecture of polygenic traits and their inter-allelic interaction. From the published information on GMA experiments in CSL, it is evident that the six-parameter model with combined scaling (individual and joint scale) test is predominantly used. The majority of the yield and its associated traits are controlled by both additive and non-additive gene effects. The non-additive effects (dominant gene) showed high magnitude with duplicate-type epistatic gene interaction, suggesting the utility of breeding methods like hybrid, heterosis, pedigree and recurrent selection for specific combining ability (RSSCA) for improvement. However, only a very few experiments were conducted in the lentil crop, although it is one of the major CSL. The GMA studies are yet to be published in the underutilised but potential legumes like horse gram.

Integrating GMA with modern plant breeding tools can enhance efficiency through validating gene action (additive, dominance and epistasis). Key integration methods include,

Genomic selection (GS)

To train the models better, the GMA data can be integrated with high-density SNP marker data, particularly when significant epistatic influence is noticed on traits where simple additive models fail to draw inference.

Molecular marker-assisted selection (MAS)

Ideal parents can be identified using GMA for desirable gene actions. The MAS tools can be used to select individuals with those traits in the segregating generations, thereby continuous phenotyping can be avoided.

CRISPR/Cas9

The identified significant specific gene interactions influencing complex traits through GMA, can be validated or muted or enhanced through CRISPR/Cas9 genome editing.

In vice versa, the newer plant breeding tools like (i) speed breeding can also be used to fasten the GMA experiments by advancing the different generations through light and or photoperiod modifications and (ii) the high-throughput phenotyping facility can be utilised for precise phenotyping of different generations for an accurate estimation of gene interaction and their effects associated with the GMA. Further, the advancements in the field of artificial intelligence (AI) and machine learning (ML) to which have the ability of detecting more complex gene interactions can also be integrated with the GMA.

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Authors' contributions

KVS conceptualised the review, carried out the literature survey and drafted the manuscript. SSJ assisted in literature collection and organisation of the content. CV and BK provided critical scientific inputs and helped improve the manuscript. RJ and RS¹ contributed to interpretation and refinement of specific sections. RS² critically reviewed, revised and finalised the manuscript. All authors have read and approved the final manuscript. [RS¹ stands for R Sivakumar and RS² stands for R Sudhagar].

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interest to declare.

Ethical issues: None

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