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# A review: Stay-green trait and its physiological and genetic basis of yield variation in rice

**Madhusmita Patra**

**Abstract**
Stay-green is one of the most significant and desirable traits which enable the crop plants to keep their green leaves in the active photosynthetic trait to maintain assimilation process and increase yield. Breeding for functional stay-green has contributed in improving crop yields, particularly when it is combined with other useful traits. This review explores the relevant literature available at national and international level on different yield attributing traits, physiological parameters and biochemical traits examined by plant breeders to sort out the most useful and promising stay green genotypes for their possible use in future breeding program. Further it has aimed to reveal the genetic variability with respect to physiological and molecular basis of stay green trait in rice. So this review has focused on various aspects like growth and growth parameters, dry matter partitioning, chlorophyll, protein and carbohydrate content, nutrient acquisition, genetic advance and heritability and correlation of grain yield with various component traits.

**Keywords:** Stay-green, senescence, quantitative trait loci, yield, grain filling, sink size

## Introduction

Rice is known as "Global Grain" and provides staple food for more than 60% of the world's population. It is the predominant dietary energy source and economically, socially as well as culturally considered important for consumers in many Asian countries, where 90% of total rice is consumed and produced. It is quite evident from the various rice improvement programmes undertaken by International Rice Research Institute that there has not been any momentous improvement in the yield potential of varieties released after IR 8 (Virmani *et al*., 1993; Khush, 1995; Peng *et al*., 1999) [93, 35, 54]. The yield stagnation is primarily due to high tillering capacity and small panicles, large number of unproductive tillers, limited sink size and lodging susceptibility. Among the various approaches suggested by the scientists to increase the yield potential, higher photosynthetic rate, slow leaf senescence, increased carbohydrate storage capacity in stems, a greater reproductive sink capacity, an extended grain filling period and tolerance to photo-inhibition are thought to be physiological basis of high grain yield (Dingkuhn *et al*., 1991) [13].

Delay of leaf senescence, also known as stay-green character, has been identified as an important component in the genetic improvement of several crops to promote stress tolerance and yield gain. Stay-green is the ability of a plant to remain green and maintain photosynthesis for longer period of time, thereby contributing photosynthates for an extended time towards grain development (Borrell *et al*., 2001) [8]. Stay-green means heritable delayed foliar senescence in crop plant species (Thomas; Thomas & Ougham, 2014) [86]. The stay-green phenotype is measured as green leaf area duration after anthesis, and is highly influenced by the time of& Howarth, 2000 [85] anthesis, with earliness tending to give an increased duration for seed filling depending on environment condition (Gregersen *et al*., 2013) [24]. The association between stay green and desirable traits such as greater number of fertile tillers (Ahlawat *et al*., 2008) [1], higher number of grains per ear (Luche *et al*., 2017) [39], tolerance to abiotic (Kassahun *et al*., 2010; Velasco Arroyo *et al*., 2016) [32, 89] and biotic (Sun *et al*., 2017) [83] stresses have been reported.

Five distinct types of stay-green plants viz. A, B, C, D and E (figure 1) have been reported where the occurrence of distinct physiological and genetic modifications can be detected (Thomas & Howarth, 2000) [85]. In Type A stay-greens, senescence is initiated late, but then proceeds at the normal rate. In Type B, senescence is initiated on schedule, but subsequently proceeds more slowly.

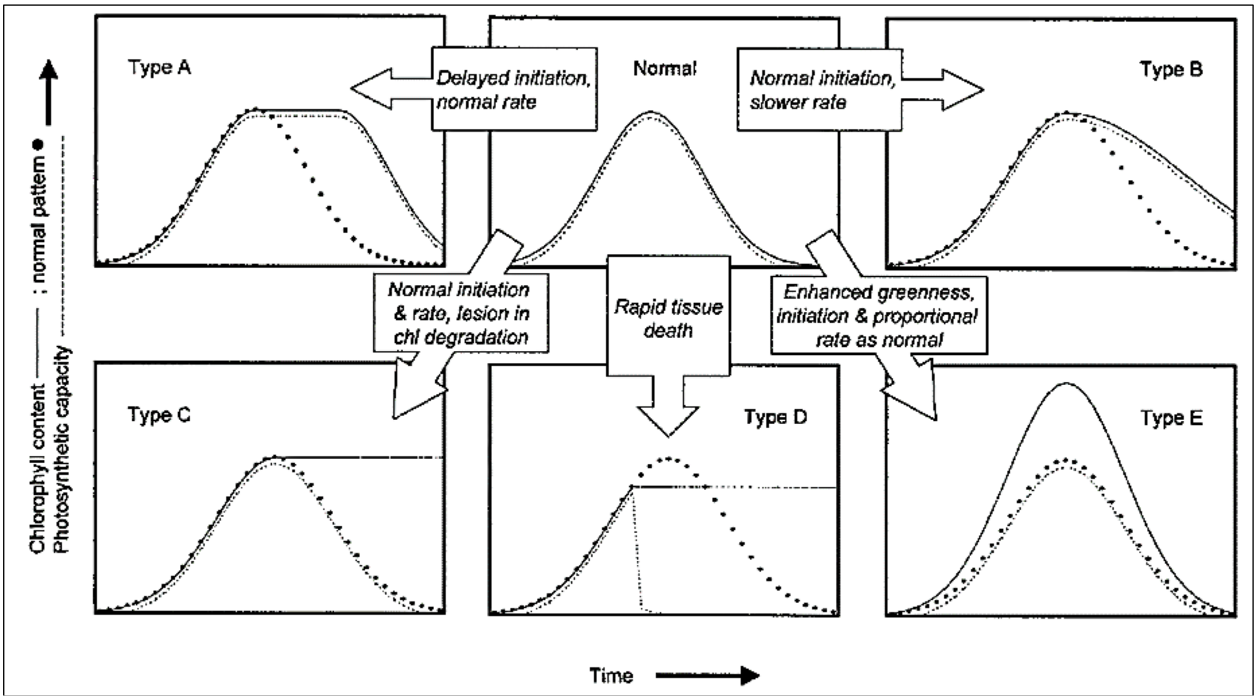


**Fig 1**. Five ways to stay-green. Curves show chlorophyll content and photosynthetic capacity (arbitrary scale) for a representative leaf, whole plant or canopy

In Type C stay-greens, chlorophyll may be retained more or less but physiological function show that senescence is proceeding normally beneath the cosmetic surface of retained pigmentation. Type D stays green are obtained by killing the leaf (freezing, boiling or drying). In Type E behaviour, the photosynthetic capacity of an intensely green genotype may follow the normal ontogenetic pattern, but comparison of absolute pigment contents identifies it as a stay-green.
The functional stay-green trait during grain filling that results from a delay in the onset of leaf senescence or a slower decrease of chlorophyll content and photosynthetic activity will probably extend the assimilatory capacity of the canopy and might contribute to higher grain yields (Gwathmey *et al*., 1992). In other words stay-green trait with slow senescence not only increase the biomass and photosynthetic efficiency but also contribute to higher seed yield by efficient translocation of photosynthates during grain filling period.
Four QTLs in rice (*Oryza sativa*) (Csfl12, TCS4, Csfl6, and Csfl9/Tcs9) were in two Recombinant inbreed lines (RILs) derived from the combination of varieties “Suweon490” (japonica and synchronized) x “SNU-SG1” (japonica and SG) and “Andabyeo” (Indica and synchronized) x “SNU-SG1” (Figure 5c). Moreover, identification of the SG QTLs Csfl6 and Tcs9 in the same positions with the two-grain yield QTLs (Yld6 and Yld9) strengthens the link between the presence of high productivity and presence of stay-green character in rice (FU *et al*., 2009) [21].

### 1. Growth and Growth Parameters

Mansab *et al.* (2003) [44] reported that for maximum crop growth, enough leaves must be present in the canopy to intercept most of the incident NAR (net active radiation). Therefore, growth is often expressed on a leaf-area basis. Samba *et al*. (2003) [66] found that interception of PAR (photosynthetically active radiation) is closely followed by LAI (leaf area index). Reduced NAR (net active radiation) interception causes reduction of the RGR and LAR. Various researchers have also reported that the genetic progress in yield potential of rice is dependent up on larger sink size, larger leaf area index (LAI) & leaf area duration (LAD) (Cheng *et al*. 2007; Peng *et al.* 2010; Yang & Zhang *et al*. 2010) [11, 95]. A number of studies indicated that increase in biomass production after flowering in rice as yield and accumulation of biomass production before flowering is a function of grain yield in rice.
The physiological character which is responsible for higher grain yield are high photosynthetic rate and slow leaf senescence (Katsura *et al.* 2007) [33] great biomass accumulation before or after anthesis (Katsura *et al*. 2007, Peng *et al.* 2009, Yang and Zhang 2010) [33, 95]. Among many agronomic characteristics, days to flowering, plant height and yield potential determine the economical production of any crop including rice (Xue *et al*. 2008). The contribution of these traits to grain yield and main yield limiting factors, however may vary with varieties, years and cropping systems (Fowlkes *et al*.,2007 Katsura *et al.*, 2007 [33] Zhang *et.al*, 2009 Peng 2010, Fisher,2011, Tian *et al*., 2011). According to Hassan *et al.* (2011), age of tillers and number of tillers per hill were significant on crop growth rate (CGR), relative growth rate (RGR), leaf area ratio (LAR) and leaf area index (LAI). Babu *et al.* (2012) [6] stated that days to flowering recorded positive and significant correlation with plant height and negative and significant association with grain yield per plant.
Panwar *et al.*, (2012) conducted a study of different rice cultivars which indicated that the growth like plant height, no. of tillers/m$^2$, leaf area index (LAI) and dry matter accumulation has positive correlation with grain yield. However during the study of inter relationship and path analysis for yield improvement in executive rice it has been concluded that the desirable traits which are responsible for seed yield, plant height, number of effective tillers per hill, flag leaf length, panicle length, biological yield per hill and harvest index (Bineeta *et al*., 2012). Plant height is the main determining factor of plant architecture which directly effect on the final yield. Other than the plant height number of tillers/plant, number of grains per panicle and grain weight

also directly effect on the final yield of rice (Selvaraj *et al.* 2011; Babu *et al.* 2012) [6].

## 2. Dry Matter and its Partitioning

Dry matter is net outcome of photosynthetic efficiency of any crop plant, accumulated in different plant parts including grain. A number of studies indicated that increase in biomass production after flowering in rice as yield and accumulation of biomass production before flowering is a function of grain yield in rice (Sahu, 2015) [64]. Song *et al*. (2012) conducted an experiment on effect of enhanced panicle nitrogen application on yield in direct seeded and transplanted rice. These results indicated that enhanced low panicle nitrogen might benefit dry matter accumulation but lead to yield decline.

## 3. Chlorophyll Content

Thomas and Howarth (2000) [85] reported that the functional stay-green trait during grain filling results from a delay in the onset of leaf senescence or a slower decrease of chlorophyll content and photosynthetic activity. Delayed senescence, or stay-green of leaf can be generally divided into two groups, functional and non-functional. The potential benefit of stay-green was initially viewed from the angle of the maintenance of photosynthetic activity (Rosenow *et al*. 1983; Thomas and Smart 1993; Borrell *et al*. 2000) [87, 8]. The stay-green trait may result from a delay in the onset of leaf senescence, from a reduced rate of senescence, or from the inhibition of one of the partial processes involved in chlorophyll breakdown (Thomas & Howarth, 2000; Luquez & Guiamét, 2001) [85, 41].

Sanchez and colleagues (2002) also made the assumption that the delayed leaf senescence from stay-green would sustain photosynthetic activity. The decrease in electron transport along photosystem II may be due to an inactivation of the oxygen evolution system or of the photosystem II reaction centre complex, as well as to the inhibition of energy transfer from carotenoids to chlorophyll (Lu *et al*., 2002) [40]. Chlorophyll is protected from degradation in contrast to soluble proteins especially in stay-green hybrids. Hörtensteiner and Kräutler (2011), told that major advances in understanding the origins and implications of stay-green followed from the discovery of the pathway of chlorophyll catabolism and associated genes growing awareness of the functional significance of the photosynthetic and nitrogen remobilization phases of leaf development. According to Kusaba *et al.,* (2013), another route to stay-green via pigment metabolism is the continued biosynthesis of chlorophyll in excess of the activity of the catabolic pathway. Plants engineered to overproduce chlorophyll-for example by overexpression of the gene encoding chlorophyllide a oxygenase.

## 4. Protein and Carbohydrate Content

Thomas and Stoddart (1995) showed that soluble protein is mobilized normally during senescence of a Festuca cosmetic stay-green, and that proteolysis could be inhibited by treatment with cytokinin or accelerated with abscisic acid (ABA), just as in the wild type, without an appreciable effect on pigment retention. Studies conducted by Fu *et al*. (2000) stated that SNU-SG1 exhibited not only higher grain-filling percentage but also re-accumulation of carbohydrate in stem at a later phase of grain filling that are presumably related to the extended duration of higher photosynthesis and the resulted increase of photosynthate translocation to grain and stem.

According to Thomas *et al.* (2002), chlorophyll is protected from degradation in contrast to soluble proteins especially in stay-green hybrids. Photosynthates generated after heading are responsible for 60-90% of the total carbon accumulated in rice panicles at harvest, while 70-90% of total panicle nitrogen uptake occurs before heading and is subsequently remobilized from leaf to grain during monocarpic senescence (Mae, 1997; Yue *et al*., 2006) [43, 97].

## 5. Nutrient Acquisition and Mobilization

As rubisco, a central enzyme for the conversion of $CO_2$ into carbohydrates, accounts for about half the nitrogen in leaves of C3 plants and about 25% of the leaves of C4 plants, remobilizing nitrogen from rubisco and photosynthetic pigments implies that the photosynthetic rate is bound to decrease during grain filling. It seems that, in contrast to species with high nitrogen sinks, the demands of developing vegetative tissue or grains can be met by nitrogen recycled from Rubisco and other soluble proteins, without recourse to the nitrogen immobilized in thylakoids as a consequence of pigment retention. (Lester, 1989; Evans, 1996; Ross-Ibarra *et al*., 2007). Hensel *et al.* (1993) [25] proposed that the switch to nutrient salvage and yellowing is a direct response to the decline in photosynthetic capacity. The percentage of phosphorus decreased rapidly after transplanting, then increased gradually and reached a high percentage at the time of the start of flowering. This high percentage continued during flowering and then decreased until the dough stage. This coincided with the translocation and accumulation of starch in the grain showing a close relationship between carbohydrate metabolism and phosphorus.

Mae (1997) [43] said that grain filling and leaf assimilation sustenance are usually conflicting processes in monocarpic cereal crops as the amount of N absorbed during grain filling is much smaller than the amount of N accumulated in mature grains. Thus, a large part of grain N is remobilized from vegetative organs especially from leaf blades to the developing grain causing leaf senescence and decrease of photosynthesis after flowering. Wade *et al.* (1999) examined the patterns of nutrient response. The effect of micronutrients was small and phosphorus, potassium was of little benefit unless nitrogen was added. But the magnitude of the nitrogen response varied substantially with water regime. According to a study conducted by Fu *et al.* (2000) nitrogen balance between the supply from remobilization and uptake during grain filling and the demand for accumulation in grain may be an important factor determining leaf senescence during grain-filling period. Inthapanya *et al.* (2000) reported that both genotypes and its interaction with fertilizer had significant effects on grain yield, which was closely associated with total N and P content at maturity. Both N and P use efficiency were consistent across fertilizer levels and hence are likely to be useful as selection criteria. They also indicated that genotypes with high harvest index are likely to perform well in different fertility conditions.

Among the five cases of stay-green reviewed by Thomas and Howarth (2000) [85], the type E stay-green is a case where senescence initiates at a similar date and follows a similar rate to a senescent type, but the higher initial nitrogen content in the leaves buffers the grain-filling-induced decline in leaf-nitrogen. That is, the current view is that an increased nitrogen uptake by roots during grain-filling leads to longer duration of leaves, and the higher specific leaf nitrogen (SLN) levels maintains the photosynthetic activity of these leaves at high levels for a longer period. In crops producing grain, the most important nutrient required to fill up grain is nitrogen and it is remobilized from the nitrogen -rich leaf tissues (Sinclair and Vadez 2002). Temporary nitrogen immobilization in rice straw hinders the nitrogen availability, but this is a temporary condition and later nitrogen becomes available by plants (Seneviratne, 2002). With rise of dry matter production phosphorus uptake increased from tillering stage to elongation stage but the phosphorus content in unit dry matter was tended to decrease in rice crop (Liu Delin *et al.*, 2005).

Thomas and Howarth, (2000) [85]; Yoo *et al.*, (2007) [96] reported that functional stay-greens are genotypes in which the carbon-nitrogen transition point is delayed, or the transition occurs on time but subsequent yellowing and nitrogen remobilization run slowly phosphorus**.** Pommel *et al.* (2006) reported that nitrogen uptake was larger and shoot nitrogen concentration decreased later in stay-green variety than the normally senescent variety during grain-filling period. It was further reported that the increment of rice yield is strongly associated with nutrient specially nitrogen, and potassium, uptake during the growth period of rice plant (Ashrafuzzaman *et al*. 2009). A study on nutrient uptake of japonica and indica rice varieties revealed that phosphorus content of rice plants in different growth stage increased with increase of phosphorus level. At maximum tillering stage there was negative correlation between phosphorus and nitrogen uptake but at harvest stage strong positive correlation was noticed. The grain phosphorus content was much higher than that of shoot (Islam *et al*., 2008). Thomas and Ougham, (2014) [86] stated that the leaves of a plant population, aggregated into a canopy, also go through carbon-capture and nitrogen-remobilization phases, although there are scaling issues that need to be considered when extrapolating results from laboratory to field.

## 6. Genotypic and Phenotypic Coefficients of Variability

**Table 1.**

| Author(s) | Character studied | Magnitude of genetic parameters | |
|---|---|---|---|
| | | PCV | GCV |
| Babu *et al.* (2012) [6] | Days to 50% flowering | Low | Low |
| | Plant height | Moderate | Moderate |
| | Panicle length | Low | Low |
| | Panicle number | Moderate | Moderate |
| | Grain number/panicle | High | High |
| | 100-grain weight | High | High |
| | Grain yield per plant | Low | Low |
| Augustina *et al.* (2013) | Days to 50% flowering | High | High |
| | Plant height | Moderate | Moderate |
| | Panicle number | High | High |
| | Grain number/panicle | High | High |
| | 100-grain weight | Moderate | Moderate |
| | Grain yield per plant | High | High |
| | Plot yield | High | High |
| Dhurai (2014) [14] | Days to 50% flowering | Low | Low |
| | Plant height | Moderate | Moderate |
| | Panicle length | Moderate | Moderate |
| | Panicle number | Moderate | Moderate |
| | Grain number/panicle | High | High |
| | 100-grain weight | Moderate | Moderate |
| | Harvest index | Moderate | Moderate |
| | Grain yield per plant | High | High |
| Rao *et al*. (2014) [91] | Days to 50% flowering | Low | Low |
| | Plant height | Low | Low |
| | Panicle number | Low | Moderate |
| | Panicle length | Low | Low |
| | Grain number/panicle | Moderate | High |
| | 100-grain weight | Moderate | High |
| | Grain yield per plant | Moderate | Moderate |
| Veni and Niveditha (2014) [90] | Days to 50% flowering | Moderate | Moderate |
| | Plant height | High | High |
| | Panicle length | Low | Low |
| | Grain number/panicle | High | High |
| | 100-grain weight | Moderate | Moderate |
| | fertility percentage | Low | Low |
| | Grain yield per plant | High | High |
| Fathelrahman *et al.* (2015) [17] | Grain yield per plant | High | Low |
| Islam *et al*.(2015) [28] | Days to 50% flowering | High | High |
| | Plant height | High | High |
| | Grain number/panicle | High | High |
| | 100-grain weight | High | High |
| | Grain yield per plant | High | High |
| Kumar *et al*.(2015) [75] | Days to 50% flowering | Low | Low |
| | Plant height | Moderate | Moderate |

| | | | |
|---|---|---|---|
| | Panicle length | Low | Low |
| | Harvest index | Low | Low |
| | Grain yield per plant | Moderate | Moderate |
| Shinde *et al.*(2015) [75] | Harvest index | High | High |
| | Grain yield per plant | High | High |
| Anis *et al.*(2016) [4] | Plant height | Low | Low |
| | Panicle length | Moderate | Moderate |
| | Panicle number | Moderate | Moderate |
| | Grain number/panicle | High | High |
| | Grain yield per plant | Moderate | Moderate |
| Mishu *et al.*(2016) [45] | Days to 50% flowering | Moderate | Moderate |
| | Plant height | Moderate | Moderate |
| | Panicle length | Moderate | Moderate |
| | 100-grain weight | Moderate | Moderate |
| | Flag leaf length | Moderate | Moderate |
| | Grain yield per plant | Moderate | Moderate |
| Jalandhar *et al.*(2017) [29] | Days to 50% flowering | Low | Low |
| | Plant height | Low | Low |
| | Panicle length | Moderate | Low |
| | fertility percentage | Low | Low |
| | Harvest index | Low | Low |
| | Grain yield per plant | High | High |
| Sumanth *et al.* (2017) [87] | Days to 50% flowering | Low | Low |
| | Plant height | Moderate | Moderate |
| | Panicle length | Low | Low |
| | fertility percentage | Low | Low |
| | Grain yield per plant | High | High |

## 7. Heritability and genetic advance

**Table 2.**

| Character | Magnitude of genetic parameters | |
|---|---|---|
| | **Heritability** | **Genetic advance** |
| Days to 50% flowering | High | High |
| | Bhadru *et al.*(2012)), Augustina *et al.*(2013), Dutta *et al.*(2013) [15], Kumar *et al.*(2013) [80], Islam *et al.*(2015) [28], Lingaraja *et al.*(2015) [38], Rajkumar *et al.*(2015) [59], Sahu *et al.*(2015) [64], Sala and Shanti (2016), Nandini *et al.* (2017) [47], Gour *et al.* (2017) [23] | |
| | **High** | **Moderate** |
| | Babu *et al.*(2012) [6], Mishu *et al.*(2016) [45], Nandini *et al.* (2017) [47], Jalandhar *et al.*(2017) [29] | |
| | High | Low |
| | Dhurai (2014) [14], Ganapati *et al.*(2014) [22], Ketan and Sarkar (2014) [34], Ogunbayo *et al.*(2014) [49], Paikhomba *et al.*(2014), Rao *et al.*(2014) [91], Sharma *et al.*(2014) [74], Shrivastava *et al.*(2014) [77], Kumar *et al.*(2015) [75], Pradhan *et al.*(2015) [55], Sarwar *et al.*(2015) [68], Senapati and Kumar (2015) [75] | |
| | **Moderate** | **Low** |
| | Savitha and Ushakumari (2015) [70], Thomas and Lal (2012) | |
| Plant height | **High** | **High** |
| | Bhadru *et al.*(2012), Ovung*et al.*(2012), Dhurai (2014) [14], Ketan and Sarkar (2014) [34], Kumar *et al.*(2014), Rajput *et al.*(2014) [60], Sharma *et al.*(2014) [74], Shrivastava *et al.*(2014) [77], Kumar *et al.*(2015) [75], Pradhan *et al.*(2015) [55], Sahu *et al.*(2015) [64], Shinde *et al.*(2015) [75], Anis *et al.*(2016) [4], Sumanth *et al* (2017) [87], Gour *et al.* (2017) [23] | |
| | **High** | **Moderate** |
| | Babu *et al.*(2012) [6], Augustina *et al.*(2013), Dhanwani *et al.*(2013),Vanisree *et al.*(2013), Lingaiah *et al.*(2014) [91], Rao *et al.*(2014) [91], Rajkumar *et al.*(2015) [59], Savitha and Ushakumari(2015) [70], Senapati and Kumar (2015) [75], Mishu *et al.*(2016) [45], | |
| | **High** | **Low** |
| | Ganapati *et al.*(2014) [22], Paikhomba *et al.*(2014), Sarwar *et al*(2015) [68] | |
| | **Moderate** | **Moderate** |
| | Fentie *et al.*(2014) [19] | |
| Panicle length | **High** | **High** |
| | Shiva Prasad *et al.*(2013), Dhurai (2014) [14], Gour *et al.* (2017) [23] | |
| | **High** | **Moderate** |
| | Ketan and Sarkar (2014) [34], Kumar *et al.*(2015) [75], Anis *et al.*(2016) [4], Mishu *et al.*(2016) [45], Jalandhar *et al.*(2017) [29], Sumanth *et al.*(2017) [87] | |
| | **High** | **Low** |
| | Babu *et al.*(2012) [6], Ovung *et al.*(2012), Shrivastava *et al.*(2014) [77], Savitha and Ushakumari(2015) [70], Sarwar *et al.*(2015) [68], Senapati and Kumar (2015) [75] | |
| | **Moderate** | **Moderate** |
| | Rao *et al.*(2014) [91], Pradhan *et al.*(2015) [55] | |
| | **Moderate** | **Low** |
| | Thomas &Lal (2012), Ganapati *et al.*(2014) [22], Nandini *et al.*(2017) [47] | |

| | | |
|---|---|---|
| | **Low** | **Low** |
| | Fentie *et al.*(2014) [19] | |
| Panicle number | **High** | **High** |
| | Augustina *et al.*(2013), Dutta *et al.*(2013) [15], Gangashetty *et al.*(2013), Shiva Prasad *et al.*(2013), Vanisree *et al.*(2013), Dhurai (2014) [14], Shrivastava *et al.*(2014) [77], Savitha and Ushakumari (2015) [70], Sarwar *et al.*(2015) [68] | |
| | **High** | **Moderate** |
| | Ogunbayo *et al.*(2014) [49], Anis *et al.*(2016) [4] | |
| | **Moderate** | **Moderate** |
| | Babu *et al.*(2012) [6], Dhanwani *et al.*(2013), Ganapati *et al.*(2014) [22] | |
| | **Low** | **Low** |
| | Singh *et al.*(2013) [80], Ketan and Sarkar(2014) [34], Lingaiah *et al.*(2014) [91], Paikhomba *et al.*(2014), Rao *et al.*(2014) [91], Pradhan *et al.*(2015) [55], Senapati and Kumar (2015) [75] | |
| No. of fertile grains/panicle | **High** | **High** |
| | Babu *et al.*(2012) [6], Augustina *et al.*(2013), Dhanwani *et al.*(2013), Singh *et al.*(2013) [80], Vanisree *et al.*(2013), Dhurai (2014) [14], Ketan and Sarkar(2014) [34], Lingaiah *et al.*(2014) [91], Rai *et al.*(2014) [91], Rajput *et al.*(2014) [60], Sandhya *et al.*(2014) [58], Saikumar *et al.*(2014), Sharma *et al.*(2014) [74], Islam *et al.*(2015) [28], Savitha&Ushakumari(2015),Sarwar *et al.*(2015) [68], Islam *et al.*(2016) [45] | |
| | **High** | **Moderate** |
| | Paikhomba *et al.*(2014), Anis *et al.*(2016) [4] | |
| | **Moderate** | **Low** |
| | Ganapati *et al.*(2014) [22] | |
| | **Low** | **High** |
| | Rao *et al.*(2014) [91] | |
| | **Low** | **Moderate** |
| | Senapati and Kumar (2015) [75] | |
| | **Low** | **Low** |
| | Fentie*et al.*(2014) [19] | |
| Fertility percentage | **High** | **High** |
| | Bhadru *et al.*(2012), Dhanwani*et al.*(2013), Ketan & Sarkar (2014) [34], Saikumar *et al.*(2014), Shrivastava *et al.*(2014) [77], Sahu *et al.*(2015) [64] | |
| | **High** | **Low** |
| | Seyoum *et al.*(2012), Sharma *et al.*(2014) [74] | |
| | **Moderate** | **Low** |
| | Vanisree *et al.*(2013) | |
| | **Low** | **Low** |
| | Senapati and Kumar (2015) [75] | |
| Grain weight | **High** | **High** |
| | Bhadru *et al.*(2012), 2013),Gangashetty *et al.*(2013), Vanisree *et al.*(2013), Dhurai (2014) [14], Fentie *et al.*(2014) [19], Ketan and Sarkar (2014) [34], Lingaiah *et al.*(2014) [91], Rai *et al.*(2014) [58], Sandhya *et al.*(2014) [58], Sharma *et al.*(2014) [74], Shrivastava *et al.*(2014) [77], Pradhan *et al.*(2015) [55], Sahu *et al.*(2015) [64], Senapati and Kumar (2015) [75], Islam *et al.*(2016) [45] | |
| | **High** | **Moderate** |
| | Babu *et al.*(2012) [6], Mishu *et al.*(2016) [45] | |
| | **High** | **Low** |
| | Ovung *et al.*(2012), Dhanwani *et al.*(2013), Singh *et al.*(2013) [80], Sarwar *et al.*(2015) [68] | |
| | **Moderate** | **Moderate** |
| | Savitha & Ushakumari (2015) [70] | |
| | **Moderate** | **High** |
| | Rao *et al.*(2014) [91] | |
| | **Moderate** | **Low** |
| | Thomas &Lal (2012), Ganapati *et al.*(2014) [22] | |
| Harvest index | **High** | **High** |
| | Sravan *et al.*(2012), Dutta *et al.*(2014), Ganapati *et al.*(2014) [22], Haque *et al.*(2014) [24], Paikhomba *et al.*(2014), Rai *et al.*(2014) [58], Sandhya *et al.*(2014) [58], Saikumar *et al.*(2014), Shrivastava *et al.*(2014) [77], Lingaraja *et al.*(2015) [38], Sahu *et al.*(2015) [64] | |
| | **High** | **Moderate** |
| | Ovung*et al.*(2012), Sharma *et al.*(2014) [74], Kumar *et al.*(2015) [75] | |
| | **Moderate** | **Moderate** |
| | Thomas &Lal (2012) | |
| | **Moderate** | **Low** |
| | Singh *et al.*(2013) [80] | |
| | **Low** | **Low** |
| | Pradhan *et al.*(2015) [55] | |
| Flag leaf length | **High** | **High** |
| | Bhadru *et al.*(2012), Sravan *et al.*(2012), Mishu *et al.*(2016) [45] | |
| | **High** | **Moderate** |
| | Sharma *et al.*(2014) [74] | |
| Flag leaf area | **High** | **High** |
| | Pandey *et al.*(2012), Sahu *et al.*(2015) [64], Islam *et al.*(2016) [45] | |

## 8. Correlation of grain yield with component traits

**Table 3.**

| Sl. No. | Character | Direction of association |
|---|---|---|
| 1. | Days to flowering | **Positive** |
| | | Bhadru *et al.*(2012), Rangare *et al.*(2012), Aditya & Bhartiya(2013), Reddy *et al.*(2013), Vanisree *et al.*(2013), Haque *et al.*(2014) [24], Sarkar *et al.*(2014) [34], Dash *et al.* (2015) [12], Islam *et al.*(2016) [45], Mishu *et al.*(2016) [45] |
| | | **Negative** |
| | | Babu *et al.*(2012) [6], Seyoum *et al.*(2012), Augustina *et al.*(2013), Singh *et al.*(2013) [80], Ganapati *et al.*(2014), Haque *et al.*(2014) [24], Haque *et al.*(2014) [24], Lingaiah *et al.*(2014) [91], Rai *et al.*(2014) [58], Kumar *et al.*(2015) [75], Pradhan *et al.*(2015) [55], Savitha & Ushakumari(2015) [70] |
| 2. | Plant height | **Positive** |
| | | Reddy *et al.*(2013), Singh *et al.*(2013) [80], Vanisree *et al.*(2013), Ganapati *et al.*(2014) [22], Haque *et al.*(2014) [24], Haque *et al.*(2014) [24], Jambhulkar *et al.*(2014) [30], Norain *et al.*(2014), Rai *et al.*(2014) [58], Venkanna *et al.*(2014), Venkatalakshmi *et al.* (2014), Dash *et al.* (2015) [12], Pradhan *et al.*(2015) [55], Savitha & Ushakumari (2015) [70], Shinde *et al.*(2015) [75] |
| | | **Negative** |
| | | Babu *et al.*(2012) [6], Bhadru *et al.*(2012), Seyoum *et al.*(2012), Augustina *et al.*(2013), Nagraju *et al.*(2013), Lingaiah *et al.*(2014) [91], Ogunbayo *et al.*(2014) [49], Ramanjaneyulu *et al.*(2014), Mishu *et al.*(2016) [45] |
| 3. | Panicle length | **Positive** |
| | | Ashfaq *et al.*(2012), Bhadru *et al.*(2012), Idris *et al.*(2012), Reddy *et al.*(2013), Sanghera *et al.*(2013), Singh *et al.*(2013) [80], Vanisree *et al.*(2013), Aditya & Bhartiya (2014), Haque *et al.*(2014) [24], Haque *et al.*(2014) [24], Lingaiah *et al.*(2014) [91], Ogunbayo *et al.*(2014) [49], Rao *et al.*(2014) [91], Dash *et al.* (2015) [12], Lingaraja *et al.*(2015) [38], Pradhan *et al.*(2015) [55], Savitha & Ushakumari(2015) [70], Islam *et al.*(2016) [45], Mishu *et al.*(2016) [45] |
| | | **Negative** |
| | | Babu *et al.*(2012) [6], Venkatalaksmi *et al.*(2014) |
| 4. | Panicle number | **Positive** |
| | | Babu *et al.*(2012) [6], Bhadru *et al.*(2012), Reddy *et al.*(2013), Sanghera *et al.*(2013), Vanisree *et al.*(2013), Ganapati *et al.*(2014) [22], Haque *et al.*(2014) [24], Norain *et al.*(2014), Ogunbayo *et al.*(2014) [49], Ramanjaneyulu *et al.*(2014), Sarkar *et al.*(2014) [34], Venkatalaksmi *et al.*(2014), Das (2015), Moosavi *et al.*(2015), Pradhan *et al.*(2015) [55], Savitha & Ushakumari(2015) [70] |
| 5. | Number of fertile grains/panicle | **Positive** |
| | | Idris *et al.*(2012), Augustina *et al.*(2013), Basavaraja *et al.*(2013), Reddy *et al.*(2013), Sanghera *et al.*(2013), Vanisree *et al.*(2013), Jambhulkar *et al.*(2014) [30], Ketan and Sarkar (2014) [34], Rai *et al.*(2014), Saikumar *et al.*(2014), Sandhya *et al.*(2014) [58], Das(2015), Dash *et al.* (2015) [12], Pradhan *et al.*(2015) [55], Savitha & Ushakumari (2015) [70], Senapati and Kumar (2015) [75], Islam *et al.*(2016) [45] |
| 6. | Spikelets per panicle | **Positive** |
| | | Rangare *et al.*(2012), Sravan *et al.*(2012) Reddy *et al.*(2013) |
| 7. | Fertility percentage | **Positive** |
| | | Satheesh kumar & Sarvanan(2012), Seyoum *et al.*(2012), Sravan *et al.*(2012), Ketan & Sarkar (2014) [34], Saikumar *et al.*(2014), Das(2015), Naseer *et al.*(2015), Pradhan *et al.*(2015) [55] |
| | | Negative |
| | | Vanisree *et al.*(2013) |
| 8. | 100-grain weight | **Positive** |
| | | Rangare *et al.*(2012), Sravan *et al.*(2012), Augustina *et al.*(2013), Ganapati *et al.*(2014) [22], Haque *et al.*(2014) [24], Lingaiah *et al.*(2014) [91], Norain *et al.*(2014), Rai *et al.*(2014) [58], Ramanjaneyulu *et al.*(2014), Rao *et al.*(2014) [91], Naseer *et al.*(2015), Savitha and Ushakumari(2015) [70], Shinde *et al.*(2015) [75], Islam *et al.*(2016) [45], Mishu *et al.*(2016) [45] |
| | | **Negative** |
| | | Reddy *et al.*(2013), Vanisree *et al.*(2013) |
| 9. | Harvest index | **Positive** |
| | | Idris *et al.*(2012), Rangare *et al.*(2012), Sravan *et al.*(2012), Nagraju *et al.*(2013), Ganapati *et al.*(2014) [22], Haque *et al.*(2014) [24], Rai *et al.*(2014) [58], Ramanjaneyulu *et al.*(2014), Sandhya *et al.*(2014) [58], Saikumar *et al.*(2014), Venkanna *et al.*(2014), Das *et al.*(2015), Kumar *et al.*(2015) [75], Lingaraja *et al.*(2015) [38], Moosavi *et al.*(2015), Pradhan *et al.*(2015) [55], Shinde *et al.*(2015) [75] |
| 10. | Flag leaf length | **Positive** |
| | | Sravan *et al.*(2012), Reddy *et al.*(2013), Norain *et al.*(2014), Dash *et al.* (2015) [12], Mishu *et al.*(2016) [45] |
| 11. | Flag leaf area | **Positive** |
| | | Pandey *et al.*(2012) |
| | | Negative |
| | | Mishu *et al.*(2016) [45] |
| 12. | Grain yield/plant | **Positive** |
| | | Dash *et al.* (2015) [12], Pradhan *et al.*(2015) [55] |

## Conclusion

During the last few years there have been tremendous increases in the understanding of the mechanisms and processes that control chlorophyll degradation in higher plants. Stay-green genotypes retained high photosynthetic competence and photochemical efficiency as well as leaf chlorophyll content throughout grain filling as compared with other genotypes. These findings revealed that the excess carbohydrates accumulated in the grain filling period in a stay-green variety is not translocated due to poor sink size, therefore it is believed that large panicles to store the increased production of carbohydrate resulting from stay-green foliage. From several findings, it has been suggested that a functional stay-green trait can be utilized for improving crop yield potential through the improved dry matter production during grain filling. There is a positive correlation between stay-green and yield as observed in several studies. Molecular techniques can be used to identify QTL controlling stay-green and its location in the chromosome. Hence it can be concluded that based on physiological, morphological and molecular characteristics, stay-green genotypes can be isolated and used in advanced breeding programmes for genetic crop improvement.

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