IMPACT OF HIERARCHY OF TILLERS ON RESOURCE ALLOCATION AND SEED PRODUCTIVITY OF SHORT AND MEDIUM DURATION RICE VARIETIES

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Abstract. Rice seed yield is determined by both the quantity and the quality of tillers. Nevertheless, not all tillers offer productivity. Especially, the late formed tillers contribute less. Understanding the limitations of late formed tillers is crucial for formulating effective tools to improve the crop yield. The current study was conducted at Tamil Nadu Agricultural University, India with two rice varieties to evaluate the hierarchy pattern of tiller development in rice to understand its relationship with the yield attributing factors. In the study, the highest number of spikelet panicle^{-1} was recorded in the primary tillers followed by the secondary and tertiary tillers, in both varieties. Between the varieties, the primary tillers of TKM-13 produced significantly higher number of spikelet panicle^{-1} (260.8) compared to CO-51 (206.2). Whereas no spikelet was recorded in the late formed tillers irrespective of the varieties. This phenomenon is attributable to the seed development and filling duration available for primary, secondary, tertiary and late-formed tillers which was 45, 30, 24 and 11 days in CO-51 and 35, 18, 14 and 15 in TKM-13, respectively. Therefore, lesser duration available for seed development in the late formed tillers is expected to have deleterious effect on seed filling.
Keywords: *tillering, flowering, spikelet, source sink ratio, seed filling*

Introduction

Rice (*Oryza sativa*) is a staple food crop consumed by over two-thirds of the global population. It is an important source of energy, vitamins, minerals, and other biomolecules although it is low in fiber and fat (Sen et al., 2020). Food and Agriculture Organization reported that an additional 30% of rice production is entailed to meet the demands of global population by 2050 (FAO, 2009). In the past few years, rice productivity seems to be stagnant especially in India, and is expected that productivity may even decline in future due to over exploitation of resources (Kumar et al., 2021). Therefore, it is vital to revisit the crop growth pattern of rice and its impact on yield attributing factors so as to frame appropriate strategies to maximize the rice yield potential for ensuring food security.

Rice is a semi-aquatic annual grass with round, hollow and jointed stems that bear panicles (culm). A mature rice plant contains a main culm and a number of side branches called as tillers. Tillering in rice, is a critical agronomic trait accountable for grain yield potential (Badshah et al., 2013; Sloan et al., 2023). Tillers are specialized grain bearing branches, that provide nutrients during the panicle development. Tillers, mainly composed of primary, secondary, tertiary branches and grains, arise from the axils of each leaf on the unelongated basal internodes in an acropetal succession (Jiang et al., 2011). The high tillering capacity is considered as a desirable trait in rice production, as number of panicles per plant is dependent on it

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(Nuruzzaman et al., 2000). It has also been contested that the higher number of tillers exhibited a greater discrepancy in mobilizing assimilates among the tillers resulting in high tiller abortion, poor grain setting, and small panicle size leading to reduction in grain yield (Penget al., 1994; Ahmad et al., 2005). Counce et al. (2007) reported that the hierarchy in tiller development i.e., primary tillers initiated from main culm, secondary tillers from primary, tertiary from secondary and so on. Among the tillers, the pattern of panicle development is hierarchical, and the grain yield becomes poorer with each tiller order. Hence, the panicles of late formed tillers do not contribute to the seed yield significantly (Wang et al., 2016). The same has been observed in other cereal crops like wheat (Otteson et al., 2008) and barley (Cannell, 1969). Short growth period of the late emerging tillers might be one of the reasons for the discrepancies in the yield among the tillers (Wang et al., 2016). Therefore, late emerging tillers are termed as unproductive tillers due to their negligible contribution to the yield potential of rice. It has been reported that, these unproductive tillers result in discontinuous nutrient and carbohydrate transportation to tillers from mother stems; moreover, they compete with reproductive tillers for nutrients in addition to light (Ao et al., 2010). Zhao et al. (2020) proposed that minimizing the number of unproductive tillers offered huge scope to enhance the harvest index in rice. It has been reported that a high ratio of productive to unproductive tillers is a desirable trait for a high yielding variety. The productive tillers and the quality of its growth rather than the number of tillers determine the panicle development, ultimately defining the yield.

Systematic Rice Intensification (SRI) is a broadly acknowledged but a controversial rice cultivation technique developed in early 1980s in Madagascar (Dobermann, 2004). SRI is a set of principles for improving the productivity and not a fixed technological package. It is proven to promote changes in the growth pattern and morphology of individual rice plants, specifically vigorous increase in the number tillers per hill than the conventional method (CM). However, it has been contested that though SRI produced higher tillering rate than the CM, it did significantly improve the rate of ear bearing tillers which could necessarily lead to high yields (Latif et al., 2009; Chen et al., 2013). Therefore, it has been argued that increase in the tillering rate leads to increased competition for the limited resources between the productive and unproductive tillers, eventually lowering yield potential of rice. Ying et al. (1998) stated that there is an inverse correlation between the total number of tillers and the number and size of panicle bearing tillers. It has also been reported that the reduction of unproductive tillers in the middle growth stages has promoted the development of heavy panicles and photo-synthetic efficiency during the later growth stages (Chen et al., 2013). Further, the main stem contributes around 35%-50% and fertile tillers contribute 50%-70% of the grain yield (Thiry et al., 2002). Therefore, any effort taken to reduce the unproductive tillers might positively influence the yield.

Against this background, a study was formulated to assess and elucidate the pattern of development of productive and unproductive tillers in two different rice varieties viz., short duration variety (CO-51) and medium duration variety (TKM-13) and to comprehend the influence of late-formed tillers in terms of yield potential of rice through assessing the tillering behavior, flowering behavior and the influence on seed filling characteristics in different orders of tillers in medium and long duration rice varieties.

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Materials and methods

Planting material and experimental site

The study was conducted in the wetland farm Tamil Nadu Agricultural university (TNAU), Coimbatore, India. The experimental area lies in the North Western agro-climatic zone of Tamil Nadu at 11°N latitude, 77°E longitude and an altitude of 426.7 m above the mean sea level. The seeds of two varieties rice (Oryza sativa) viz., CO 51 (Short duration of 105 to 110 days) and TKM 13 (Medium duration of 125 to 130 days) were provided by the Department of Rice, TNAU, Coimbatore and the laboratory experiments were performed at the Department of Seed Science and Technology, TNAU, Coimbatore. The study was started on first fortnight of November 2023 and ended on first fortnight of March 2024. The weather during the growing condition is given in *Figure 1*.

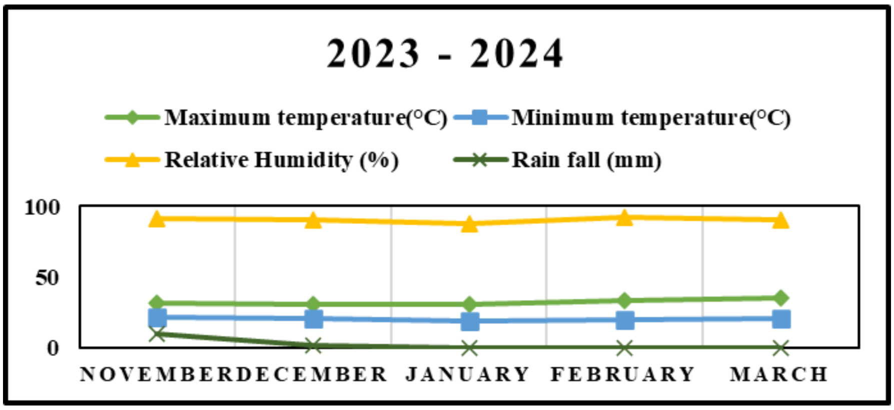

Figure 1. *Meteorological data of the examined season*

Cultivation and crop management

Nursery

The rice seedlings were raised in wet nursery bed by adopting the conventional method, by sowing the seeds of each variety in individual beds. Nursery beds were manually constructed with a spade and soil was thoroughly pulverized with hoe. After pulverizing and leveling of bed surface, 10 kg of vermicompost, 100 g urea and di-ammonium phosphate and 50 g of Murate of potash were well mixed and applied uniformly over the bed. The seeds of each variety were soaked overnight before sowing, separately. The sprouted seeds were sown uniformly over the nursery seed bed which was covered by a thin film of water in. The seedlings of 14 days old were pulled for transplantation.

Main field

The experimental plots of 15 × 3 m^2 were prepared for each variety. Fourteen days old seedlings of each variety were transplanted on to the individual plots with the spacing of 25 × 25 cm, separately. Recommended dose of fertilizers (120:40:40 kg of NPK ha^{-1} and 150:50:50 kg of NPK ha^{-1} for CO 51 & TKM 13, respectively) were applied. Irrigation was given depending on soil condition (till a hair line crack appeared) up to vegetative stage and later on water layer up to 2.5 cm was maintained

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till physiological maturity. The soil was not allowed to dry out throughout the crop period. The irrigation was stopped 15 days prior to harvest and water was drained from the field to hasten grain hardening process.

Observations

Tillering and flowering characteristics

After transplantation, the experimental crop raised in individual blocks in the main field was observed periodically to record the date of emergence of primary, secondary and tertiary tillers. Growth characteristics were recorded in 5 plants for one replication and 5 replications were adopted. The traits of days to tillering and flowering of primary, secondary, tertiary, and late formed tillers plant^{-1}, number and height (cm) of primary, secondary, tertiary, and late formed tillers plant^{-1} were recorded. The recordings were done on five randomly selected and tagged plants and the mean was noted. Likewise, the number of tillers per m^2 were counted at 5 places and the mean was recorded with 5 replication.

Physiological characteristics

The physiological characteristics *viz.,* flag leaf area and flag leaf chlorophyll content were recorded during 50% flowering stage with five randomly selected plants. The aforementioned traits were recorded for primary, secondary, tertiary, and late formed tillers separately for each variety. The flag leaf area was measured using linear method (Leaf area = b × l× w: b = Leaf area factor (for rice 0.65), l = Leaf length and w = leaf width). The chlorophyll content was recorded using SPAD- 502 (soil and plant analysis development) chlorophyll meter, it quantifies the green color immediately by non-destructive measuring method (Dwyer et al., 1991).

Yield characteristics

The yield characteristics *viz.,* number of spikelet panicle^{-1}, number of filled seeds panicle^{-1}, number of ill-filled seeds panicle^{-1} of primary, secondary, tertiary, and late formed tillers were recorded separately, recordings were done on five randomly selected plants and the mean was noted with 5 replications. The trait of 1000 seed weight (TSW) (g) in the panicle was arrived with weighing of eight replications of 1000 seeds of primary, secondary, tertiary, and late formed tillers separately in analytical balance as per ISTA (2011) and the mean was expressed as g 1000 seeds^{-1}.

Statistical analysis

The data obtained from experiments were analyzed with ANOVA (Analysis of variance) as described by Panse and Sukhatme (1985) in MS excel i.e. two factor ANOVA. Tillering hierarchy was taken as one factor and the rice varieties were taken as another factor. Also run Pearson correlation at $P < 0.05$ in SPSS 20.0.

Results

The present study involved two rice varieties *viz.*, CO-51, a short duration variety of 105 to 110 days and TKM-13, a medium duration variety with the total growth period of 125 to 130 days.

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Tillering and flowering characteristics

The tiller emergence in CO-51 and TKM-13 was initiated on 30 and 36 days after sowing (DAS), respectively and it was extended up to 80 and 85 DAS respectively. Although the days to tiller initiation varied only by 6 days between CO-51 (30 DAS) and TKM-13 (36 DAS), the flower initiation was delayed by 15 days in TKM-13 compared to CO-51 (*Table 1*). The active tillering stage in CO-51 and TKM-13 was attained on 48 and 55 DAS, respectively following that the tiller emergence in CO-51 and TKM-13 started to decline (*Fig. 2*). The decline in the tiller emergence was evident after the completion of emergence of secondary tillers (*Figs. 3* and *4*). In the variety CO 51, the number of competing tillers for resources increased after 42 DAS. The tertiary and late formed tillers constituted 19.86 and 19.19% respectively and in the variety TKM 13, the number of competing tillers for resources increased after 47 DAS. The tertiary and late formed tillers constituted 19.87 and 18.9% respectively (*Figs. 3* and *4*). The height of tillers was found to decrease with the hierarchy of tillers i.e., Primary > Secondary > Tertiary > Late formed tillers, irrespective of varieties (*Fig. 5*). The flower initiation started by 65 and 80 DAS while it was completed by 99 and 115 DAS in CO-51 and TKM-13, respectively (*Table 1*). Height of the tillers was found to decrease along the hierarchy. The primary tillers recorded the maximum height in CO-51 and TKM-13. The number of spikelets per panicle was highest in the primary tillers of both varieties and the late formed tillers recorded null spikelets (*Fig. 5*).

Table 1. *Days to tillering and flowering of primary, secondary, tertiary and late-formed tillers of the rice varieties CO-51 and TKM-13*

Hierarchy of tillers	Days to tillering		Days to flowering	
	CO-51*	**TKM-13****	**CO-51***	**TKM-13****
Primary	30	36	65	80
Secondary	42	46	80	97
Tertiary	57	62	86	101
Late- formed	68	73	99	115

*****Short duration variety (105 to 110 days). **Medium duration variety (125 to 130 days)

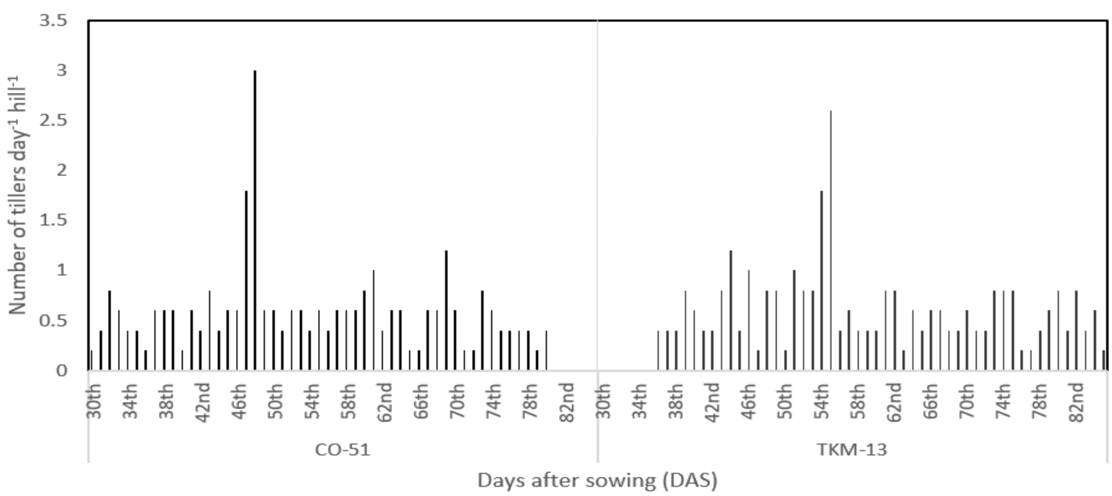

Figure 2. *Number of tillers emerged per plant per day in rice varieties CO-51 and TKM-13*

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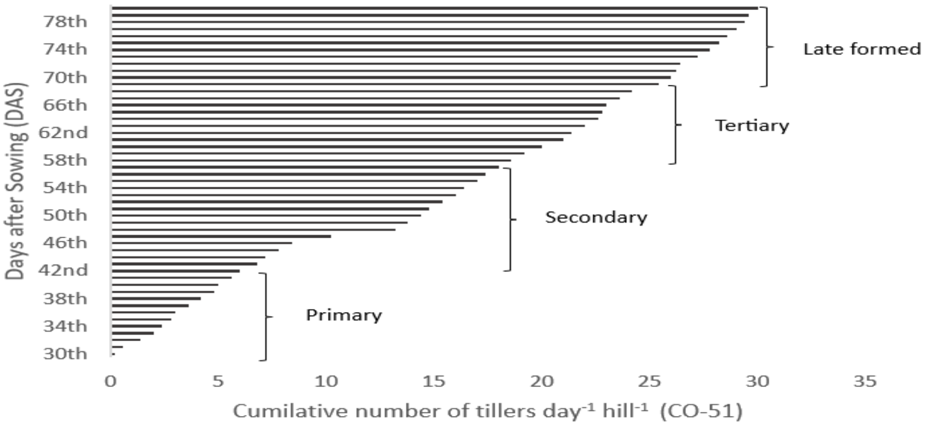

Figure 3. *Number of tillers per plant in different days after sowing (DAS) in CO-51*

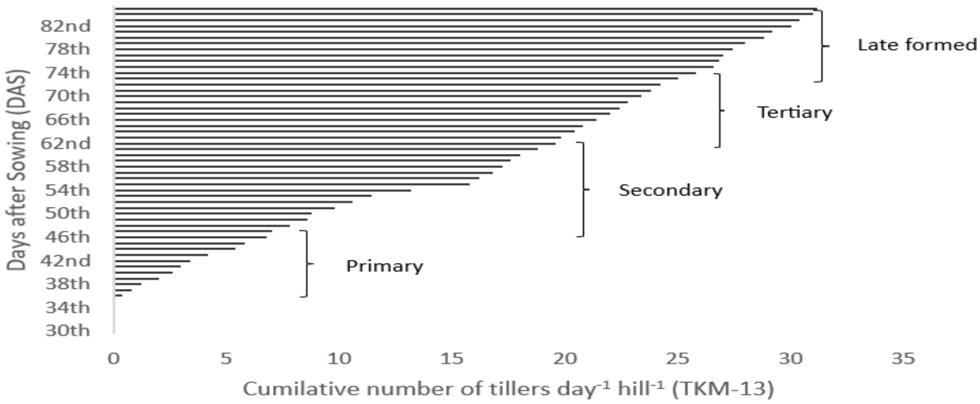

Figure 4. *Number of tillers per plant in different days after sowing (DAS) in TKM-13*

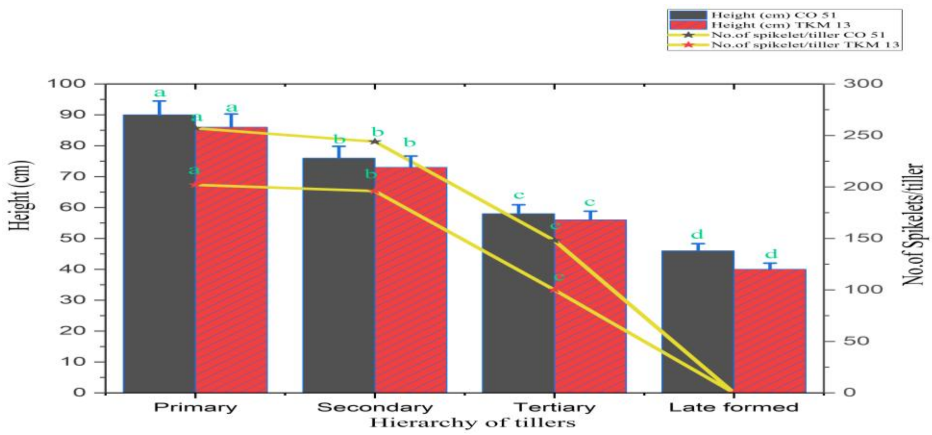

Figure 5. *Impact of hierarchy of tillers on tiller height and number of spikelets per panicle in rice varieties*

Physiological characteristics

Flag leaf area indicates the photosynthetic ability of the leaf and it plays a major role in providing energy to the developing grains. Therefore, larger the flag leaf area, better will

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be its photosynthetic ability. In the present study, the flag leaf area of both the varieties was highest in the primary tillers (29.2 and 45.3 cm^2) and lowest in the late formed tillers (12.0 and 16.8 cm^2), in CO-51 and TKM-13 respectively (*Fig. 6*). Between the varieties, the primary tillers of TKM-13 recorded the highest flag leaf area (45.3 cm^2) than CO-51 (29.2 cm^2). The chlorophyll content at 50% flowering stage was denoted by the SPAD value (*Fig. 6*). The primary tillers of CO-51 and TKM-13 recorded the highest chlorophyll content of 46.3 and 47.6, respectively followed by the secondary tillers. A significant reduction in the SPAD value was observed in the tertiary (41.2 and 40.2) and late formed tillers (38.3 and 38.0) of CO-51 and TKM-13 respectively.

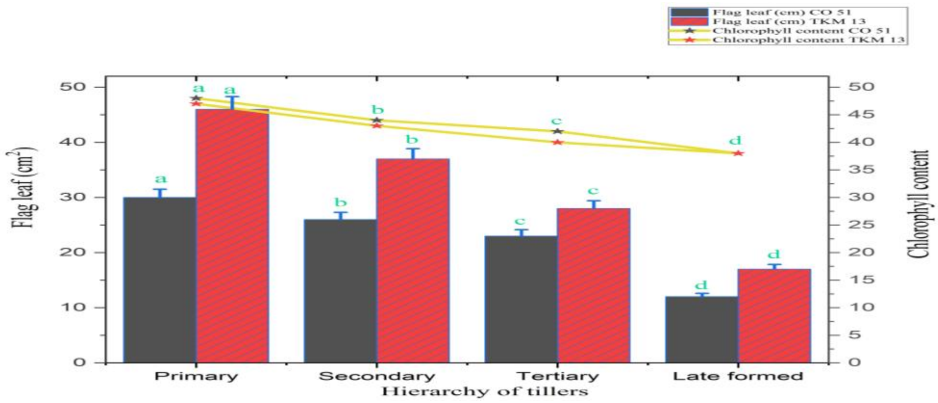

Figure 6. *Impact of hierarchy of tillers on flag leaf area (cm²) and chlorophyll content of rice*

Yield characteristics

The highest number of spikelet $panicle^{-1}$ was recorded in the primary tillers of CO-51 and TKM-13 followed by the secondary and tertiary tillers. Between the varieties, TKM-13 produced significantly highest number of spikelet $panicle^{-1}$ (260.8) in the primary tillers, followed by CO-51 (206.2). Considering the late formed tillers, no spikelet was observed irrespective of the varieties (*Fig. 5*). Among the hierarchy of tillers, the highest values of the number of filled seeds $panicle^{-1}$ were observed in the primary tillers of both the varieties, however TKM-13 (218.4) recorded significantly higher value than CO-51 (172.6) (*Fig. 7*). The number of filled seeds $panicle^{-1}$ was found to be decreasing with the hierarchy of the tillers, while the number of ill-filled seeds $panicle^{-1}$ increased. The highest number of ill-filled seeds $panicle^{-1}$ was recorded in tertiary tillers of TKM-13 (68.1) and CO-51 (43.2) followed by secondary and primary tillers. The late formed varieties of both varieties did not produce either filled or ill-filled seeds (*Fig. 7*). The TSW (g) recorded in primary (14.07), secondary (12.02) and tertiary (11.40) was found to be lower in TKM-13 compared to CO-51 tillers which recoded 21.13, 20.38 and 19.65 respectively. The maximum 1000 seed weight was recorded in the primary tillers of both varieties and it was found to decrease as the tiller order increased (*Fig. 8*).

Discussion

In the current study, the primary tiller initiation was observed on 30^{th} and 36^{th} DAS in CO-51 and TKM-13, respectively. The emergence of secondary, tertiary and late-formed tillers was delayed by 12, 27 and 38 days in CO-51 and by 10, 26 and 37 days in

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TKM-13, respectively. Eventually, the flowering in secondary, tertiary and late-formed tillers was also delayed by 15, 16 and 34 days in CO-51 and by 17, 21 and 35 days in TKM-13, respectively (*Table 1*). Taking the total crop duration into consideration, it can be noticed that the seed development and filling duration available for primary, secondary, tertiary and late-formed tillers was 45, 30, 24 and 11 days in CO-51 and 35, 18, 14 and 15 in TKM-13. Prakash and Kumari (2021) reported that the grain filling efficiency decreases with the tiller order with lower grain filling in the late formed tillers. In the current study, reduction in the duration available for seed development and filling as per the tillering hierarchy is expected to have deleterious effect on the seed filling, number of filled and ill-filled seeds per panicle (*Fig. 7*). It has been reported that the contributions of late emerging tillers to the seed yield was significantly lower than the main stem or early emerging tillers (Wang et al., 2017). Wang et al. (2016) also established that yield discrepancies in rice crop was mainly due to the emergence of late formed tillers. On an average, 96% of primary, 76% of secondary and only 32% of tertiary tillers produced panicles (productive tillers), hence it might be best to prevent the initiation of late tillers or develop a variety eliminating the late emerging tillers (Kim and Vergara, 1991). Further, the correlation between tillering and flowering window of test varieties (*Tables 2* and *3*) proved that hierarchy of tillers have positive effects on seed filling sources thus influenced the seed yield of both rice

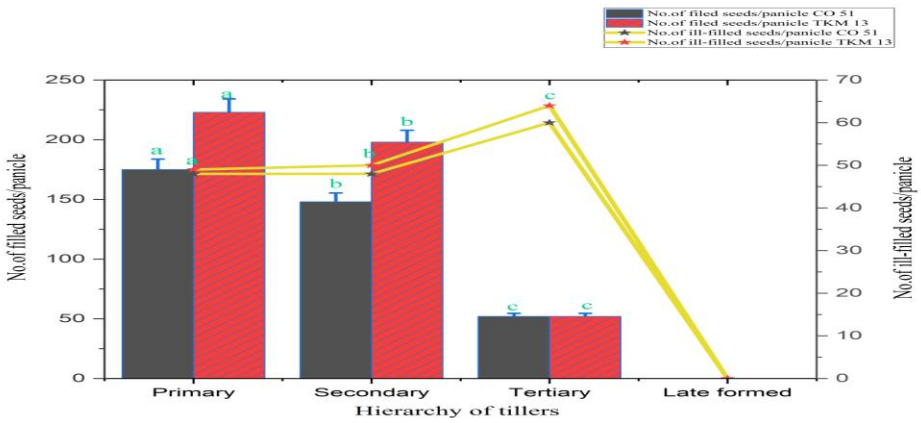

Figure 7. *Impact of hierarchy of tillers on filled and ill-filled seeds of rice varieties*

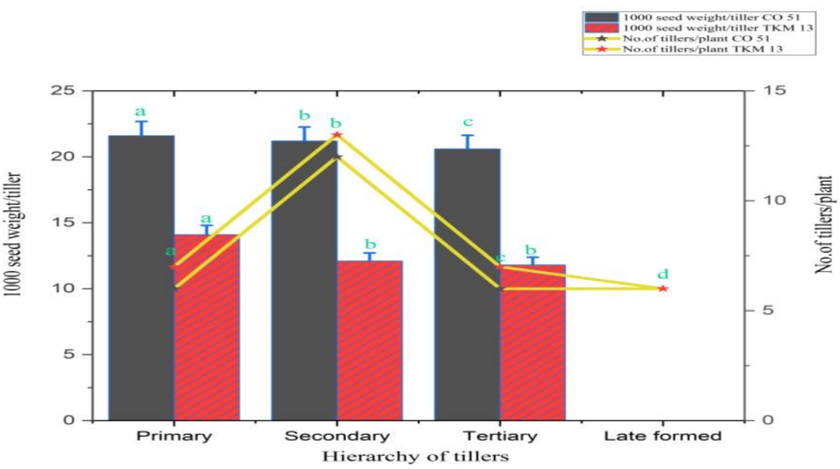

Figure 8. *Impact of hierarchy of tillers on number of tillers and 1000 seed weight of rice*

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Table 2. *Correlation of tillering and flowering window on seed filling efficiency of rice variety CO 51*

	NTs	NSt	NFS	FSP	SFD
NTs	1				
NSt	0.466	1			
NFS	0.430	0.999**	1		
FSP	0.496	0.999**	0.997**	1	
SFD	0.083	0.685	0.903**	0.868	1

NTS - No. of tillers; NSt - No. of spikelets; NFS - No. of filled seeds; FSP - Filled seeds (%); SFD - Seed filling duration in days. *$p < 0.05$; **$p < 0.01$. Data were averaged across the crop duration and observed parameters)

Table 3*. Correlation of tillering and flowering window on seed filling efficiency of rice variety TKM 13*

	NTs	NSt	NFS	FSP	SFD
NTs	1				
NSt	0.584	1			
NFS	0.571	0.999**	1		
FSP	0.630	0.998**	0.997**	1	
SFD	0.097	0.765	0.873*	0.834	1

NTS - No. of tillers; NSt - No. of spikelets; NFS - No. of filled seeds; FSP - Filled seeds (%); SFD - Seed filling duration in days. *$p < 0.05$; **$p < 0.01$. Data were averaged across the crop duration and observed parameters)

Flag leaf, the uppermost leaf beneath the panicle is a major source photosynthates during reproduction and seed filling period, since it has a significant role of delivering photosynthates to the emerging grains, it is critically important for panicle development and thereby determining the grain yield potential (Rahman et al., 2013). The marginal advantage of the high yielding group in the photosynthetic rate at a leaf level gets amplified due to the significantly higher flag-leaf area and total leaf area per plant. This leads to potentially a higher canopy photosynthesis in the high yielding group compared with the low yielding group (Vishwakarma et al., 2024). As current photosynthesis is the key component of source strength, the optimization of unit leaf photosynthesis and canopy photosynthesis is critical for improving source strength in rice (Vishwakarma et al., 2023). Therefore, larger the flag leaf area better will be the yield. Present study indicated that, flag leaf of the primary tillers of the varieties CO-51 and TKM-13 were larger compared to other tillers in the hierarchy, indicating that the primary tillers were more effective in aiding the filling in seeds. It has been reported that flag leaf area and panicle length are positively co-related thereby reflecting on the yield potential (Li et al., 1998; Bing et al., 2006). The results are in conformity with the findings of Ekamber et al. (2012), who reported that the older tillers have larger flag leaf area compared to the newer tillers, with smaller area recorded in the recently formed tillers.

Additionally, chlorophyll content is an important determinant of rice yield (Ramesh et al., 2002). In the present study, the SPAD value of primary tillers of CO-51 and TKM-13 recorded the highest compared to the late-formed tillers of the respective varieties. The difference in the photosynthetic ability of leaves on the tillers will have an

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impact on the spikelet development (Zhang and Yamagishi, 2010). The flag leaf of secondary and tertiary tillers had lower concentrations of photosynthetic pigments and proteins than the older tillers (Ekamber et al., 2012; Zhou et al., 2022). Hence, the combination of better flag leaf area and chlorophyll content had a positive impact on the number of spikelet panicle^{-1} and ultimately the seed yield of the primary tillers of both varieties, proving the fact that early emerged tillers are vital for the rice yield potential. Sarkar et al. (2002) has reported that rice yield is dependent on the leaf chlorophyll content.

Number of spikelet panicle^{-1} is the most important determinant of rice yield (Duy et al., 2004). It has been reported that spikelet number per panicle decreases with the tiller order from primary and secondary tillers to tertiary (Zhang and Yamagishi, 2010; Yan et al., 2023). The results of current studies evidently proves that the number of spikelet panicle^{-1} decreases with the hierarchy of the tiller with null spikelet in the late formed tillers, irrespective of the varieties studied. Extent of decrease observed in the tertiary tillers over primary tiller was 49.8% and 49% in CO-51 and TKM-13, respectively. Nevertheless, as none of the late emerging tillers produced any spikelet thus wastefully competing for the available limited resources for seed filling thereby detrimentally affecting the number of filled seeds produced in the early formed tillers. In terms of sink strength, rice crop yield depends upon grain number per unit area and the test weight of grain. Grain number per panicle, and thus grain number per plant, was a major contributing factor for grain yield in the HY group, while test weight was similar between the HY and LY groups (Li et al., 2019). In the current study, a decrease in the number of filled seeds was observed with proportionate increase in the number of ill-filled seeds along the hierarchy of tillers. TSW is a direct determinant of rice yield which in turn is determined by the filling efficiency. In the present study, TSW was found to be highest in the primary tillers of CO-51 (21.13) and TKM-13 (14.07). Mohapatra and Kairali (2008) reported that, the seed yield of the panicle of main shoot was the highest among the tillers and yield of the successive tillers declined in a sequence. The TSW recorded in the secondary tillers were 3.53% and 14.57% decrease over the primary tillers of CO-51 and TKM-13 respectively. With respect to tertiary tillers of CO-51 and TKM-13 the per cent decrease observed was 7 and 18.97%.

Conclusion

The data revealed that the primary and secondary tillers were in more advantageous position with respect to number of days available for seed development and filling compared to tertiary and late-formed tillers. Further the flag leaf area and the chlorophyll content (SPAD values) were also found to be higher in the early formed tillers. It has been clearly established that the late-formed tillers including the tertiary tillers are less productive in terms of number of spikelet panicle^{-1}, number of filled seeds panicle^{-1} and TSW in both short (CO-51) and medium duration (TKM-13) varieties. Thus, competing for available limited resources.

The results of the present study envisages that breeding of new rice varieties should be oriented towards the objective of attaining optimum number of tillers and lengthier panicles in order to obtain higher number of panicles per unit area so as to increase the rice productivity. Alternatively, appropriate agronomic practices may also be developed to eliminate of the emergence of unproductive tillers by reducing the plant spacing or by formulating potential foliar spray fluids which can cause cessation of tiller production

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post active tillering stage. These practices can reduce the wasteful competition from unproductive tillers and increase the productivity potential of early formed tillers in terms of a greater number of spikelets panicle^{-1}, filled seeds panicle^{-1} and higher TSW and eventually increasing rice yield per unit area. The research paper lays a strong foundation for the need of effective management of source-sink ratio to achieve improvement in rice productivity.

Author contributions. Conceptualization & Methodology VV. Formal analysis, ND. Investigation, ND. Resources & Data curation ND, PSV. Writing-original draft, VV, ND & RB. Writing-review & editing, RB &UR. Visualization, ND &PSV. Supervision, VV. Project administration, VV. Funding acquisition VV. All co-authors reviewed the final version and approved the manuscript before submission.

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