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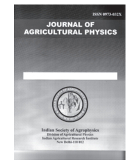

Research Article

Yield and Panicle Growth of Rice (*Oryza sativa*) Tillers in Relation to Canopy Status at Different Nitrogen Levels

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ABSTRACT

Influence of nitrogen on panicle growth of mother, primary and secondary tillers of rice were examined with 2 rice cultivars differing in their response to nitrogen viz 'IR36' (high nitrogen responsive) and 'Swarnaprabha' (low nitrogen responsive). The panicle group analysis was done depending on the height (main shoot and tiller height) and growth stage by separating into two strata with respect to their position in canopy, i.e., the lower (two third) and upper (one third of canopy by height) of each shoot. Panicle groups differed in single panicle weight, grains per panicle and panicle growth rate. Higher dose of nitrogen decreased the contribution of the upper canopy stratum to total grain yield, however contribution from tertiary tillers increased from 9.6% (N_0) to 20.55% (N_{90}). Yield increase in high nitrogen responsive cultivar 'IR36' was associated with increase in panicle number while in low nitrogen responsive cultivar 'Swarnaprabha' it was due to increase in grain number per panicle and percentage of total grain yield in upper canopy. Hence it is suggested that selection of breeding lines and nutrient management practices which encourage low but early tiller number with panicle in the upper canopy would be beneficial in increasing yield potential of rice in future.

Key words: Canopy location, *Oryza sativa*, N application, N responsiveness, reproductive growth, Yield component analysis

Introduction

Documentation of yield distribution in various canopy strata of the rice (*Oryza sativa* L.) plant is necessary for the simulation studies that relates crop yield to resource partitioning and growth parameters within the canopy (Matthews and Wassmann, 2003; Choudhury, 2001). Increased understanding of the factors that influence yield and modifying factors on yield component distribution in the plant may aid in breeding for plant types with improved canopy architecture and in crop management (Ying *et al*., 1998). Yield distribution patterns have been described in general (Kropff *et al.,* 1993, Shiratsuchi *et al.,* 2005; Leuning *et al.,* 2000) for high yielding (Osaki *et al.,* 1991), and for tiller groups (Padmaja Rao, 1994) and canopy stratum (Dingkuhn *et al.,* 1992).

One of these processes that greatly influences rice yield is tillering. Tillers are branches that arise from the leaf axil at nodes of a main stem or a tiller stem, which are termed primary, secondary or tertiary tillers, respectively. Hanada (1993) showed that the number of tillers of rice was greater under low temperature conditions than under high temperature conditions. Yan *et al.* (2010) observed that compared with transplanted lowland rice, the low tillering and tiller productivity in our experiment could have resulted from higher air temperatures. The emergence and development of tillers at low

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phytomer orders 1st–3rd were delayed or aborted. Consequently, the tiller buds at middle and higher orders (including elongated internodes) broke dormancy and developed into tillers. It has been reported that tillers that early emerging tillers contribute more to grain yield than tillers that emerge later (Counce *et al*., 1996).

Rice tillering is a major determinant for panicle production and as a consequence affects total yield. Tillering is an essential factor when estimating yield, but investigations rarely include the temporal changes that occur in tillers. The timing and frequency of flowering tillers complied with rules of priority depending on their order, rank and emergence time (Jaffuel and Dauzat, 2005).

The substantial variability observed in responses of rice varieties to tillering is closely related to plasticity with respect to nutritional management and environmental conditions. Dingkuhn *et al*. (1992) found that even at the low nitrogen level more yield was contributed by the tillers which extended into upper canopy levels. Nitrogen treatment and nitrogen responsiveness of the cultivar influenced the vertical distribution of yield components in part due to influences on the location and contribution of yield bearing tillers (Weerakoon *et al*., 2005). The present study was undertaken to investigate further the contribution of tillers to yield and the influence of N application on the distribution of yield and yield components in the various panicle groups at different canopy levels.

Materials and Methods

Location ad experimental design

Cultivars 'IR 36' - a high N responsive (Thiyagarajan *et al.,* 1991) and 'Swarnaprabha' - a low N responsive (Narasinga Rao and Murty, 1987) were planted on January 15th (*rabi* seasons) for 2 consecutive years (2008 and 2009) at NRRI, in a deltaic alluvial sandy loam soil (Haplaquept). The plants were at normal spacing (20 × 15 cm). The experimental design was Randomized Block Design with four replications. Nitrogen in the form of urea was applied at 0, 60 and 90 N/ha (designated as N_0, N_{60} and N_{90}) in 3 splits basal, active tillering and panicle initiation stage and Phosphorous @ 30 kg/ha and potash @ 20 kg/ha was applied basally. The tillers ('IR 36' and 'Swarnaprabha') were tagged as P1, P2, P3, ... and S1, S2, S3, ... for primary and secondary tillers representing their chronological sequence of emergence.

Panicle group analysis

The panicle group analysis was done depending on the height (main shoot and tiller height) and growth stage by separating into two strata with respect to their position in canopy, i.e., L- the lower (two third) and U- upper (one third of canopy by height) of each shoot. Nine panicle groups consisting of one mother shoot, four primary and four secondary tiller groups were thus created for each sample categorized by their origin and spatial position. A schematic representation of them is given in Fig.1.

Panicle growth characteristics

Beginning with the Flowering at five days interval, panicles were sampled, counted, dried, weighed, threshed and the spikelets were counted. Panicle Growth Rate was taken to be the slope of the line (fitted by least square technique) of single panicle weight vs. time for the flowering to harvest sampling dates. Effective filling period

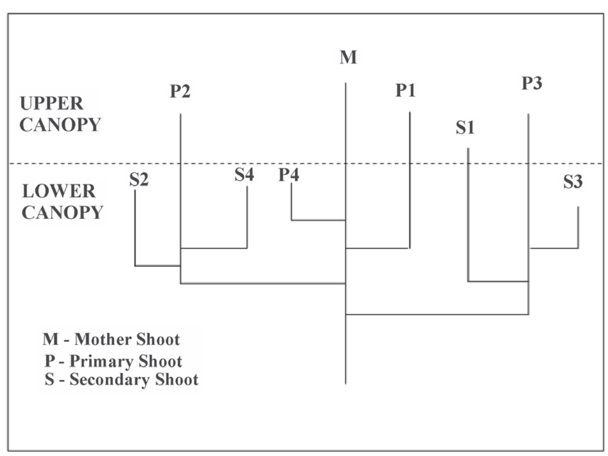

Fig. 1. Schematic representation of the nine panicle groups
M - Mother shoot, P - Primary shoot and S - Secondary shoot

was the quotient of single panicle weight from the final sampling date derived by panicle growth rate.

Statistical analysis

An analysis of variance for randomized block design was performed. Panicle groups and sampling dates were considered as further treatments in the design. Due to the absence of panicle in some groups, Grain per panicle, Panicle growth rate, single panicle weight and effective filling period could not be calculated in all instances. Where this occurred for 20% or more of the data points for a group within a treatment, that group was excluded from the analysis. As there was no significant difference between the data from both the years a pooled ANOVA was calculated for all the analysis mentioned below. Data from the nine-panicle group were also analysed in two other combinations. For the *Canopy strata analysis*, panicles were considered from (i) L- lower two third and (ii) U- upper one third of the canopy. For the *tiller origin analysis*, three categories of panicles were compared (i) panicles on the mother shoot (M), (ii) panicle on primary tillers (P) (tillers originating from the mother shoot) and (iii) panicles on the secondary tillers (S) (tillers originating from the primary tillers).

Results and Discussion

The differences between cultivars, among the N levels, between primary and secondary tillers were significant in respect of total spikelets, percentage of filled spikelets, panicle growth rate and yield. Similarly significant differences were observed between upper and lower stratum in respect of total spikelets, percentage of filled spikelets, panicle growth rate and yield. Nitrogen application significantly ($P<0.05$) increased yield in 'IR 36- a high N responsive cultivar' (Table 1). There was no significant yield difference between treatment N_{60} and N_{90} in 'Swarnaprabha – low N responsive cultivar'. Plant height during the sampling dates (Table 1) increased with high N application. Similar observations were made with the number of panicles from the primary and secondary tillers, but the difference between

Table 1. Grain Yield, plant height, number and distribution of panicle for different Nitrogen application of rice cultivars

Cultivar	Yield			Plant height**			Panicle number*								
							Upper stratum			Lower stratum			Total		
	N0$^{\psi}$	N60	N90	N0	N60	N90	N0	N60	N90	N0	N60	N90	N0	N60	N90
	g/plant			mm			Number/plant								
'IR 36'	6.83	15.66	21.43	620	734	781	4.3	5.1	5.0	0.9	3.2	4.1	5.1	8.2	9.0
'Swarnaprabha'	15.89	19.23	19.85	771	846	875	2.9	3.8	4.2	1.0	2.4	2.3	3.9	6.2	6.3
LSD (Nitrogen)$^{\psi\psi}$	1.37(2.45)			46.15(82.43)			0.3 (0.4)			0.7 (0.9)			1.1		
LSD (Cultivar)	1.37(2.85)			46.13(95.95)			0.2 (0.4)			0.5 (0.8)			0.9 (1.2)		

* - Panicle number was divided into strata, based on tiller height

** - Plant Heights and panicle number were averaged over sampling dates

$^{\psi}$ - N0 - 0kg N, N60 = 60 kg N and N90 = 90 kg N/ha

$^{\psi\psi}$- P ≤ 0.05 (values in parenthesis are at P d" 0.01)

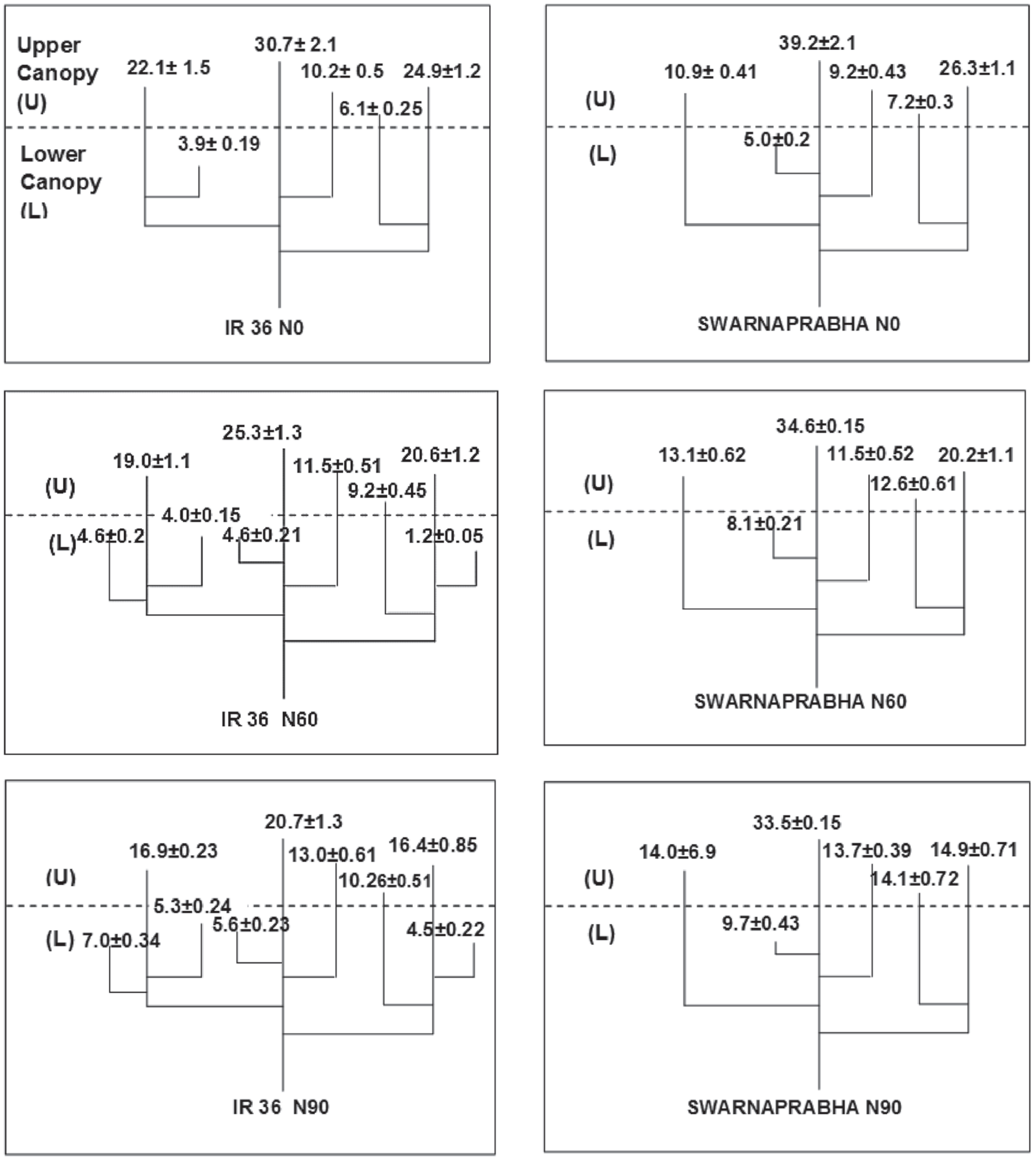

Fig. 2. Percentage of total sample yield at each of the nine panicle groups as influenced by nitrogen and N responsiveness (cv.IR 36- hign N responsive and cv.Swarnaprabha - low N responsive) of the cultivar. The lease significant difference (P<0.05) between panicle groups was 3.56

high and low N responsive variety was less significant. The panicle number in the primary and secondary tillers increased with high N application. Low N treated plants were more advanced (about 15 days) in reproductive growth stage than high N treated plants. Higher proportion of grain yield was contributed by the panicle of the mother shoot (Padmaja Rao, 1994). From our study it is observed that primary branches contribute substantially to yield in low and high yielding environments.

Panicle group analysis

When the yield of each panicle group was expressed as a percentage of total sample yield then sampling date did not significantly change the yield distribution. Percent yield was significantly different among the panicle groups and the interactions of group with N responsiveness and with N application were significant ($P<0.05$). The total yield contribution (Fig. 2) of the mother shoot in both the cultivars decreased from 34.98 at control to 27.16% at N_{90}.

Most of the primary tiller yield was in the upper canopy, but the proportion of yield contributed by the primary tiller panicle in the upper stratum decreased with high N application and with N responsiveness of the variety. Tillers in the lower stratum contributed substantially to yield with an increased contribution at high N (N_{90}) application.

Panicle in the upper canopy due to N application contributed about 86.53 and 92.39% of yield (Fig. 2) in IR36 and Swarnaprabha respectively. N application increased the proportion of (EBT %) in the lower stratum. The grain yield in all the treatments was mostly confined in the upper one third of the canopy. The upper canopy stratum contributed approximately 95.5, 88.8 and 83.9% of the yield for N_0, N_{60} and N_{90} treatments respectively. The correlation coefficient between the percent yield and percent of filled grain weight of the panicle group was very high (r=0.99* for both years).

Canopy stratum affected the yield significantly. In general upper canopy stratum contributed by abut 89.3% of the total yield whereas only 10.7% by the lower canopy. Within the upper and lower canopy stratum mother, primary and secondary tillers yield contribution was about 34.6, 54.2 and 11.2 and 52.0, 48.0 and 0% respectively. In total the contribution of mother, primary and secondary tillers to the total yield was about 26.8, 55.4 and 17.9% respectively.

Shifts in pattern of yield distribution with N responsiveness have been reported (Shiratsuchi *et al.,* 2005). In general, increased N responsiveness resulted in increase in the proportion of yield on tillers as opposed to that on main axis. Leuning *et al.* (2000) reported that panicles in the upper one third of canopy generally contributed more for the yield. However in this study, panicles on tillers originating from the lower canopy yielded more grains with increased N responsiveness whereas the contribution of the other tillers in the upper canopy decreased. Narasingha Rao (1987) in their study observed that low nitrogen responsive Swarnaprabha contains less number of tillers. In our study we observed that in Swarnaprbha most of the panicles were in the upper canopy, which compensate for low tiller number. Variability in N application may also change the panicle yield distribution pattern (Dinghkuhn *et al.,* 1992). N application increased the development of primary/secondary tillers into the upper canopy resulting in higher panicle yield.

Panicle characteristics

Panicle growth rate and single panicle weight were about 10% less for panicle in the lower two third of the canopy stratum than for the other group (Table 2). N application and its interaction with the panicle group were not significant ($P>0.1$) for panicle growth rate and single panicle weight. Although there were no detectable differences in panicle growth rate and single panicle weight among the N_0, N_{60} and N_{90} treatments, there was a significant ($P< 0.05$) cultivar by group interaction. Differences in panicle growth rate and single panicle weight between panicles in different groups were smaller in N_0 than in N_{90}. Single panicle weight for secondary tillers of panicles positioned in the lower canopy strata were smaller than in other groups, but panicle growth rate did not differ among panicle groups. In this study, the yield increase in high nitrogen environment was accompanied by increase in development of secondary tillers in the lower canopy and the yielding ability of the panicles located in the lower canopy. Effective filling period ranged from 27 to 30 days with no detectable difference ($P>0.1$) among N responsiveness of the variety, N application, nor panicle groups.

Canopy strata analysis

The data were analyzed according to the canopy stratum in which panicles were located, panicle growth rate, single panicle weight and spikelets per panicle (based on total spikelets) were smaller in the lower two third of the canopy (Table 2). There was a significant interaction between nitrogen, stratum at $P<0.1$ for panicle growth rate and at $P<0.05$ for single panicle weight. Effective filling period was not influenced by N application on stratum. The reductions in single panicle weight and panicle growth rate

Table 2. Panicle growth rate, panicle weight and spikelets/panicle for different Nitrogen application

		Panicle growth rate mg panicle^{-1} day^{-1}			Single panicle weight[1] (g)			Spikelets / panicle					
								Filled grains			All spikelets		
group[2]	stratum	N0[3]	N60	N90	N0[3]	N60	N90	N0[3]	N60	N90	N0[3]	N60	N90
Panicle group													
U M	81.21	95.36	117.73	2.44	2.95	3.54	99	125	148	121	169	174	
U	P1	62.42	86.19	97.08	1.8	2.66	2.93	74	121	124	99	146	166
U	P2	54.99	82.19	102.31	1.61	2.51	3.06	61	102	134	85	141	152
U	P3	41.45	53.66	65.24	1.22	1.61	1.94	55	83	113	74	96	121
U	S1	30.59	31.88	50.89	0.95	1.28	1.59	54	72	93	74	88	111
L	P4	30.55	43.71	55.64	0.94	1.33	1.66	40	61	72	60	76	96
L	S2	...	13.12	15.66	...	0.29	0.45	..	13	25	..	41	54
L	S3	...	11.55	13.73	...	0.35	0.43	..	13	20	..	35	50
L	S4	...	...	11.21	...	...	0.35	..	..	15	..	..	48
LSD N Treatment[4]			ns (ns)			ns (ns)			20.17 (ns)			ns(ns)	
LSD group			22.26 (32.26)			0.21 (0.29)			24.63 (ns)			ns (ns)	
Canopy stratum													
U		49.61	53.75	77.26	1.59	2.31	2.62	68	101	122	90	128	145
L		29.17	29.96	35.1	0.94	1.13	1.31	41	51	63	61	76	99
LSD N treatment			ns (ns)			ns (ns)			30.7			ns (ns)	
LSD stratum			20.36 (15.54)			1.35 (0.9)			40.63 (50.3)			ns (ns)	
Tiller group													
M		81.21	95.36	117.73	2.44	2.96	3.54	96	126	148	121	169	174
P		47.35	66.44	80.07	1.39	2.03	2.4	58	92	111	80	116	134
S		30.59	30.32	43.57	0.92	1.18	1.42	55	57	86	74	82	107
LSD N treatment			ns (ns)			1.9 (ns)			ns (ns)			50.86 (ns)	
LSD tiller			ns (ns)			1.5 (1.2)			ns (ns)			ns (ns)	

1. Single panicle weight from final sampling date
2. Panicle strata in canopy, L & M = lower two third & upper one thirds respectively of canopy; Panicle origins: M = panicle on main axis, P1, P2, P3, P4 and S1, S2, S3 & S4 = panicle on primary & Secondary tillers originating in its chronological order
3. N0 = No N applied, N60 = 60 kg N ha^{-1} and N90 = 90 kg N ha^{-1}
4. P≤0.05 (values in parenthesis are at P≤0.01)

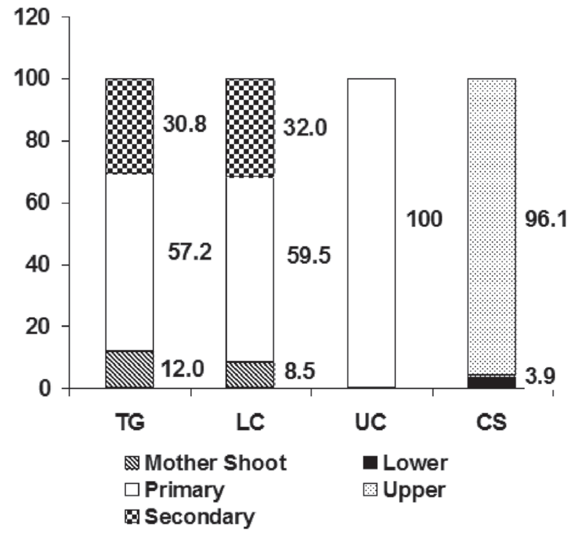

Fig. 3. Effect of (i) Canopy stratum and (ii) Tiller origin on percentage of total sample yield as influenced by N responsiveness (cv.IR 36 - high N responsive & cv.Swarnaprabha - low N responsive) and N treatment

were found in the lower canopy stratum, perhaps due to attenuation of irradiance or spectral changes in the spectral distribution of light in the lower canopy as suggested by Leuning *et al.* (2000).

Tiller origin analysis

When the data were analyzed according to the tiller origin (mother shoot panicle vs. panicle on tillers), single panicle weight was significantly influenced by origin (Table 2). The single panicle weight for panicle on the tillers in the lower third of the canopy was smaller (P<0.05) than for panicle on main shoot or other tillers, and the nitrogen application by origin interaction was significant. Effective filling period in the N_{90} treatment (32 days) was greater (P<0.05) than in the control (27 days). Secondary and late primary tillers contribute little to grain yield as they are located in the lower canopy stratum and actually have a negative effect on the productivity.

Yield and its components

The effect of N application on yield and yield components is dependent on the amount of N applied (Shiratsuchi *et al*., 2005). A decrease in panicle number by N_0 can be compensated with increased in spikelets per panicle and or single panicle weight if high N (60 or 90) is applied. In this study the number of filled grains, effective filling period did not substantially increase by N application. Whereas spikelets per panicle, single panicle weight and panicle growth rate were similar for different N levels. Panicle number has been found to be strongly associated with yield in rice, suggesting that number of panicle per unit area is more important than for example grain number or single panicle weight.

Spikelet number decreased over the sampling period for N_0, N_{60} and N_{90} irrespective of N treatment (Fig. 4). A high percentage of spikelets were chaffy in N_{90} than in N_{60} and compared to other panicle groups, the lower canopy stratum contained a high percentage of chaffy grains. When values for spikelets per panicle were calculated based on total spikelets, then spikelets per panicle generally increased with N application and decreased for panicles in the lower stratum (Table 2). The spikelets per panicle values calculated on the basis of only the filled grains, there were no detectable differences (P>0.05) between nitrogen, variety and panicle groups.

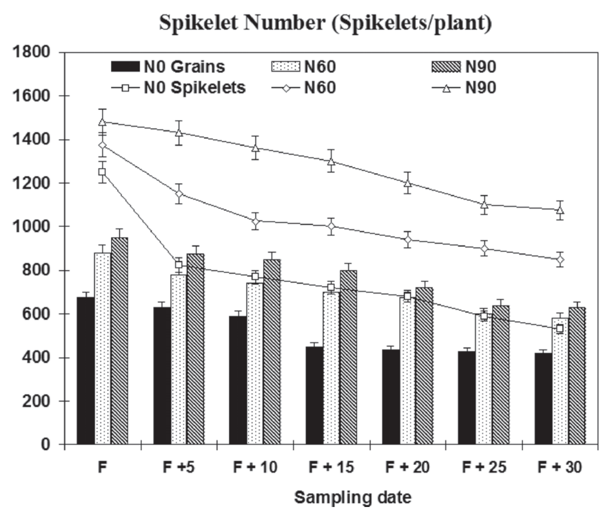

Fig. 4. Number of total spikelets and filled grains as influenced by sampling date and N application. Total spikelets included filled spikelets plus chaffy spikelets. Values were averaged over cultivars. The least significant difference (P<0.05) between N treatments for total spikelets was 54.10, for filled grains LSD was 47.90. F – Flowering

Spikelets number declined from the first sampling date with the extent of the decline greater in N_0 than in N_{90} (Fig. 4). The number of the filled grains was more consistent than total spikelet number over the sampling dates. It suggests that many of the small-unfilled spikelets may have abscessed as suggested by the results of Leuning *et al.* (2000). The percentage of poorly filled spikelets was greater in tillers of secondary origin and those of lower canopy stratum than those of primary and upper canopy stratum.

Conclusions

Variability in rice yield was observed in tiller origin and canopy strata analysis. The principal changes appeared relative to their nutrient management and the varietal response. Panicle groups differed in single panicle weight, grains per panicle and panicle growth rate. Higher dose of nitrogen decreased the contribution of the upper canopy stratum to total grain yield, however contribution from tertiary tillers increased from 9.6% (N_0) to 20.55% (N_{90}). Yield increase in high nitrogen responsive cultivar 'IR36' was associated with increase in panicle number while in low nitrogen responsive cultivar 'Swarnaprabha' it was due to increase in grain number per panicle and percentage of total grain yield in upper canopy. Hence it is suggested that selection of breeding lines and nutrient management practices which encourage low but early tiller number with panicle in the upper canopy would be beneficial in increasing yield potential of rice in future.

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