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Time of emergence determines the pattern of dominance of rice tillers

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Abstract

A large number of later-initiated tillers of semidwarf rice cultivars become either less- or un-productive at maturity. Rice cultivar Lalat was grown in pot (2001-02, Sambalpur University) and field (2004, Regional Research and Technology Transfer Station, Chiplima). The phenological and morphological development, assimilate contents and grain yield of the panicle of different categories of tillers were assessed in order to find out the bias against development of the less productive tillers. The order of dominance of the tillers decreased acropetally in both the conditions. In contrast to the field, the plant tillered profusely in pots. The duration of vegetative and reproductive periods of the late-initiated tillers were short as events like tiller emergence, booting and anthesis were delayed in them, but maturity date was more synchronized. Among tillers, panicle grains yields and assimilate concentration decreased with durations of vegetative and reproductive growth. The concentration of soluble sugars was highest at anthesis and differed among the classes of tillers with lower concentration in the late-initiated tiller compared with the early-initiated tillers. The concentration of soluble sugars at anthesis correlated positively with grain yield. Absence of late-tillers in the field-grown plants increased dominance of early-tillers and prompted higher partitioning of assimilates to panicle at crucial stages like booting and anthesis for benefit of grain yield. In contrast, late-emerged tillers of the potted plants having biomass less than 2.5 g possessed poor sink organogenesis and failed to use assimilates partitioned in their favour to achieve reasonable grain filling.

Key words: assimilates; dominance; emergence; grain yield; panicle; rice; spikelet; tillers

Introduction

Rice yields increased considerably when IR8 and subsequent cultivars of similar type were released in late 1960s. In semidwarf rice, high and early-tillering capacity is considered beneficial for grain yield (De Datta, 1981; Yoshida, 1981). A profusely tillering cultivar has the advantage of being able to be planted at a wide range of spacing without any adverse influence on the grain yield. However, the grain yield of semidwarf rice has not increased significantly since the 1970s with the absence of any genotypic modification of plant type (Flinn et al., 1982; Kropff et al., 1994). Recently it has been proposed that a new plant type with only 3-4 tillers per plant and a large number of high-density grains per panicle should be developed (Peng et al., 1999; Vergara et al., 1990). However, selecting a genotype with a few large tillers may not achieve the objective of high yield unless assimilates are mobilized into the spikelets for adequate filling. For example, the *japonica/indica* hybrid rice had a large number of unfilled grains due to poor partitioning of assimilates (Yang et al., 2002; Yuan, 1994).
Development of tillers in rice is asynchronous with the primary tillers producing more good quality grains compared to the secondary or tertiary tillers that initiate later (Vergara et al., 1990). The numbers of vascular bundles in rice tillers decrease Acropetally from the primary to the tertiary tillers

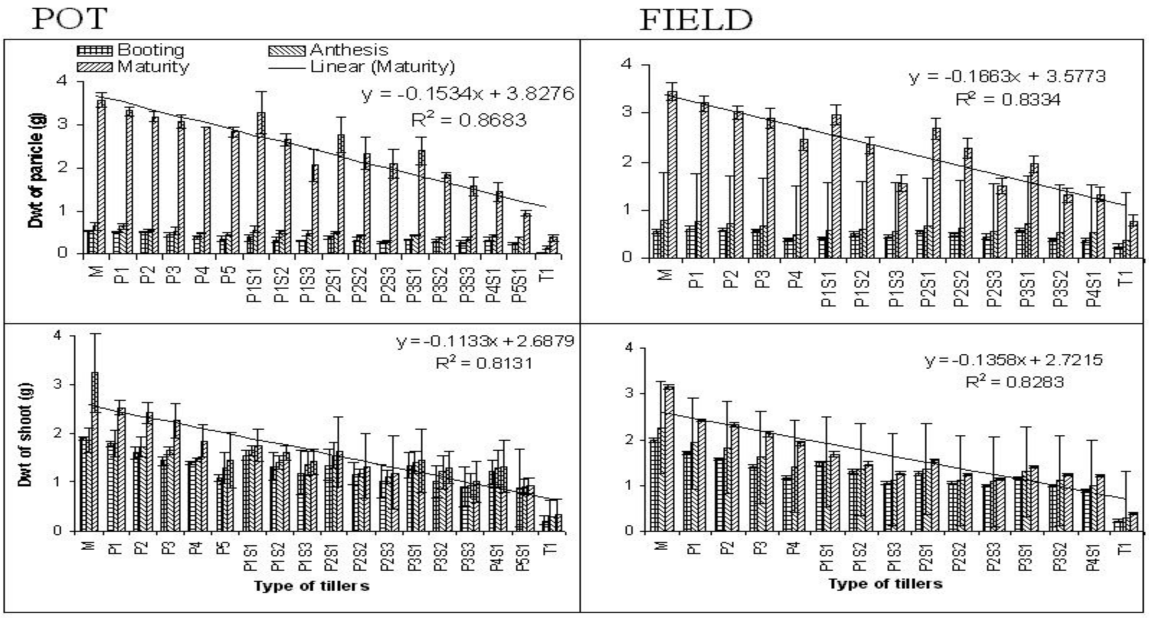

Fig1. The dry mass of panicles (top) and shoots (bottom) of different type of tillers at booting, anthesis and maturity in rice cultivar Lalat grown in pots (left) and in the field (right). The vertical bars represent ± one standard deviation (n =3). The regression line has been drawn at maximum values (maturity).

(Hayashi, 1976), and late-initiated tillers may not have an adequate number of vascular bundles to sustain the growth of the spikelets on their panicle (Kim and Vergara, 1991). Poor vascularisation reduces the supply of assimilates and hormones from the source leaves to the panicle, and thereby, significantly restricts spikelet development. A tiller gains photosynthetic independence after emergence from the preceding leaf sheath. It then transports assimilates to the sink organs growing at the apex, but at the same time, it competes with other tillers for light and nutrients. In rice, the manipulation of tiller number is important for grain yield, but the physiological basis of the regulation of tiller growth remains unclear. In general, large tillers result in higher sink:source ratio, spikelet number, proportion of filled grains, leaf area per tiller and sink capacity (Choi and Kwon, 1985). In a field study, a low-tillering/large-panicled rice genotype was reported to have an 8% yield advantage over a profuse-tillering genotype when both the genotypes were grown under high nitrogen conditions (Kim and Vergara, 1991). In maize and sorghum, the increase in yield potential resulted from increases in sink size and a decrease in tiller number (Khush, 1990). In the new rice plant type, increased dominance of the early-tillers is encouraged to preclude the production of late-tillers by genotypic modification. Preclusion of unwanted tillers is also possible by manipulation of environmental parameters (De Datta, 1981; Yoshida, 1981). The objective of the present experiment was to study the intrinsic factors responsible for variation in tiller growth resulting in the formation of different grades of tillers (Fig.1) in a semidwarf high-yielding *indica* rice cultivar in two environments that affected phenology and tillering. In the process, the physiological factors regulating tiller dynamics are identified and suggestions made in the improvement of the plant type for rice. Additionally, attempt was made to find out threshold time and biomass necessary for sustaining tiller yield in a multi-tillered rice cultivar.

Materials and methods

Plant material and Cultivation

A high yielding semidwarf *indica* rice (*Oryza sativa* L. cv. Lalat) was grown in concrete pots placed in the open air at the School of Life Sciences, Sambalpur University, Jyoti vihar, India during the dry season of 2001-02. The cultivar was also grown in the field during the 2004 wet season

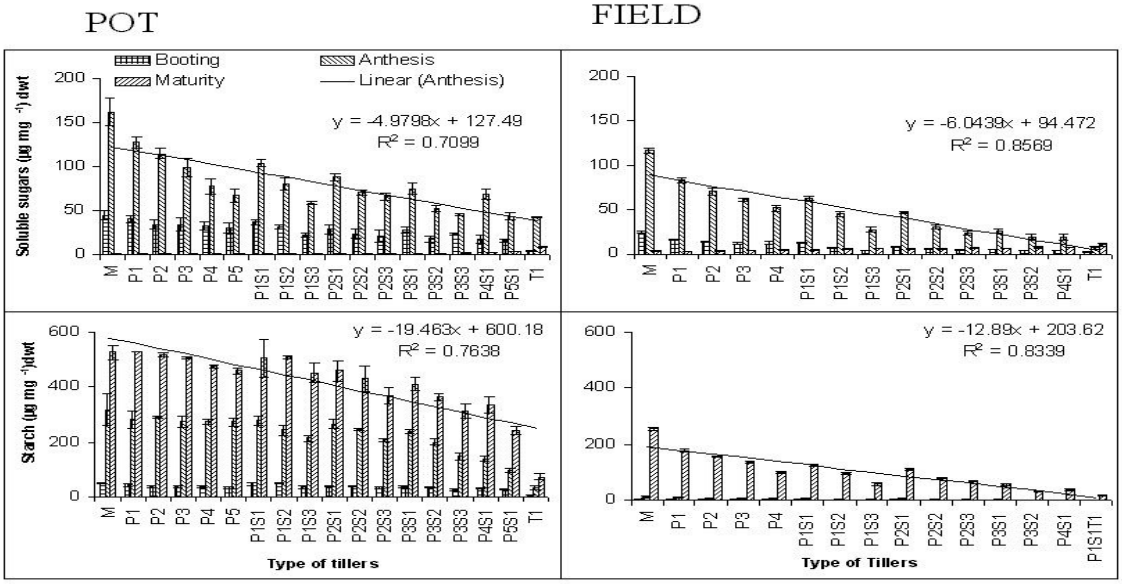

Fig 2. The concentration of soluble carbohydrates (top) and starch (bottom) in the panicles of different type of tillers at booting, anthesis and maturity in rice cultivar Lalat grown in pots (left) and in the field (right). Vertical bars represent ± one standard deviation (n =3). The regression line has been drawn at maximum values (carbohydrates at anthesis and starch at maturity).

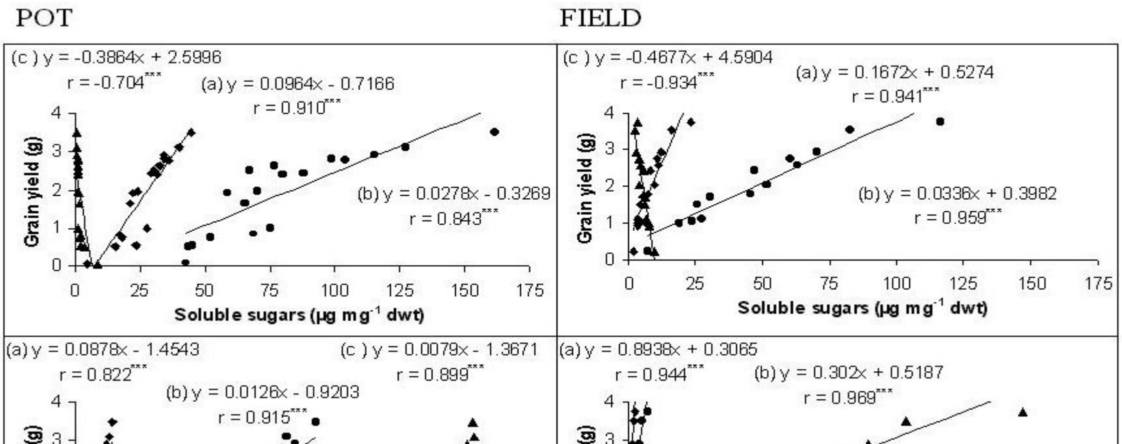

Fig 3. Relationships between soluble carbohydrate concentration and grain yield at maturity (top) and starch concentration and grain yield at maturity (bottom) of different type of tillers of high yielding rice cultivar Lalat cultivated under pot (left) and in the field conditions (right). The equations in parentheses (a), (b), and (c) represent the data for booting (rectangle), anthesis, (circle) and maturity (triangle) respectively.

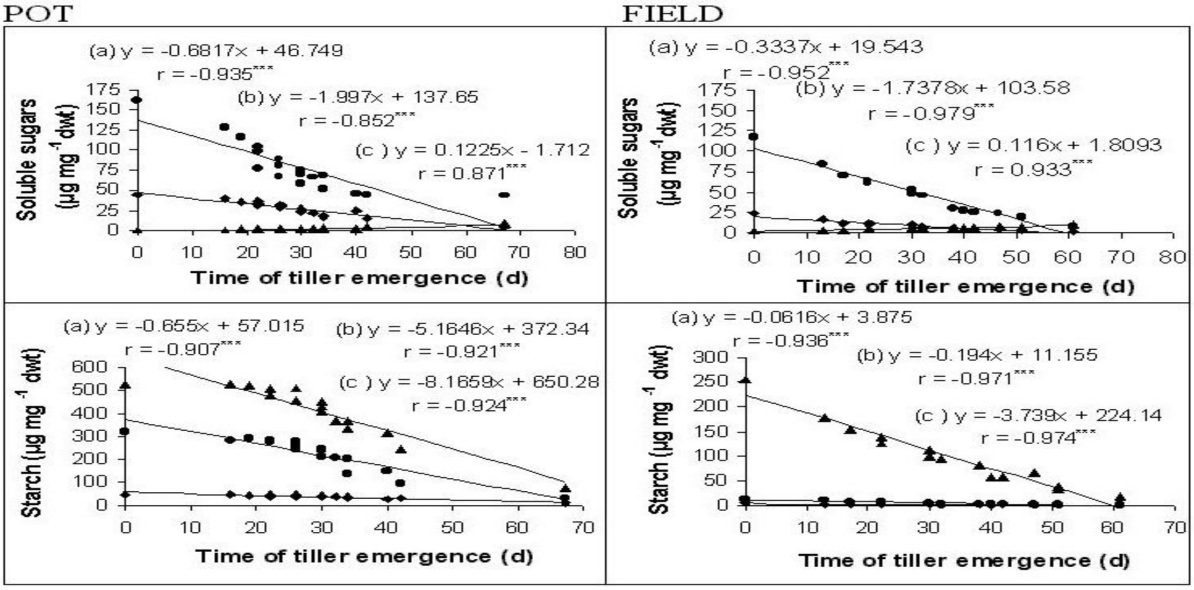

Fig 4. Relationships between time of tiller emergence and soluble carbohydrate concentration (top) and time of tiller emergence and starch concentration (bottom) of different type of tillers of high yielding rice cultivar Lalat cultivated under pot (left) and in the field condition (right). The equations in parentheses (a), (b), and (c) represent the data for booting (rectangle), anthesis, (circle) and maturity (triangle) respectively.

at the Regional Research and Technology Transfer Station, Orissa University of Agriculture and Technology, Chiplima, India. The cultivar is photo-insensitive and belongs to the medium-duration group (120 days). Under normal conditions, it produces a large number of tillers. The pots were arranged in a randomised block design with three replicates in 3 X 3 blocks with 9 pots in each block. The experiment in the field condition was designed with RBD and the experimental area was divided into 3 X 3 identical blocks (4 X 3m) and each block contained 9 small plots. Seedlings were raised in a nursery bed before transplanting into pots or field. Seedlings with uniform growth and development were only used for the culture. Seven days after transplantation, plants were thinned to 4 plants per pot to give a density of approximately 36 plants/m^2. Each pot (330 x 330 x 260 mm) contained 42 kg of sandy loam soil supplemented with commercial fertilizers consisting of N, P_2O_5 and K_2O in the ratio of 80:40:40 applied at the time of transplanting (one quarter N, full P and half K), tillering (half N) and panicle initiation (one quarter N and half K). In the field the fertilizers were applied in the same ratios and at the same stages. The level of surface water in the pots and field was maintained at 5 ± 2cm. Regression analyses and correlations between different morphological and physiological parameters were worked out using computer Microsoft Excel programme.

Morphological observations and Sampling

The main shoot and primary, secondary and tertiary tillers of each plant were tagged by counting the leaves. The height of the tillers was measured weekly from the day of tiller emergence. The panicle of the fertile tillers was severed from the neck node at booting, anthesis and maturity. The fresh weight of the panicle and shoot were recorded. Putting them into an oven at 90^{o}C for one hour followed by gradual reduction of temperature to 37^{o}C in 24 h dried the plant materials. The materials were kept in the oven for 48h more before estimation of dry weight. The leaf area was derived through multiplication of the length of leaves and width at half height by a factor 0.69 and the tiller height was the distance between the point of origin and the summit of the highest leaf or panicle (Yoshida, 1981). The grain yield components of the varieties were recorded in three replicates at the time of maturity. The time of visual panicle initiation (about 11 days after panicle initiation) and maturity (yellowing of 90 to 100% filled grains) were determined according to the procedure of De Datta (1981). Spikelets without a developed

Table 1. **Morphological and phenological features of the semidwarf rice cultivar Lalat grown in pots in 2001-2002.** TE, tiller emergence; PI, visible panicle initiation; BT, booting; AN, 50 % anthesis; MA, maturity. Date of sowing and transplanting: 10.12.2001 & 17.1.2002. Total grain weight: 47.2 ± 4.3 g. (± SD, n =3)

Type of tillers	**Days from transplanting**					**Length of panicle (cm)**	**Number of grains**		**Weight of fertile grains (g)**	**% yield contribution (g)**
	TE	**PI**	**BT**	**AN**	**MA**		***Fertile***	***Sterile***		
M	0	64	77	81	121	27.7 ± 0.5	157.3 ± 08.1	21.3 ± 3.2	3.47 ± 0.2	7.4
P1	16	66	77	81	121	27.2 ± 0.3	150.0 ± 01.5	22.7 ± 2.5	3.10 ± 0.4	6.6
P2	19	68	79	83	121	26.8 ± 0.3	141.0 ± 08.9	25.7 ± 2.9	2.90 ± 0.1	6.2
P3	22	70	79	83	121	26.5 ± 0.0	134.0 ± 10.2	26.0 ± 2.7	2.81 ± 0.5	5.9
P4	22	70	79	83	121	25.7 ± 0.6	125.0 ± 05.7	29.3 ± 4.9	2.63 ± 0.1	5.6
P5	26	74	81	85	123	25.3 ± 0.6	118.7 ± 15.6	31.7 ± 0.6	2.48 ± 0.1	5.3
P1S1	22	70	79	83	121	26.0 ± 0.1	129.3 ± 12.3	27.0 ± 3.5	2.76 ± 0.2	5.9
P1S2	26	74	81	85	123	25.7 ± 0.3	114.7 ± 08.5	35.0 ± 7.9	2.40 ± 0.1	5.1
P1S3	30	77	83	87	123	24.3 ± 0.8	107.3 ± 07.2	37.0 ± 8.7	1.90 ± 0.1	4.0
P2S1	26	74	81	85	123	25.3 ± 1.1	117.0 ± 02.7	32.7 ± 4.5	2.41 ± 0.0	5.1
P2S2	30	77	83	87	123	23.5 ± 0.8	107.3 ± 03.5	38.0 ± 2.7	1.96 ± 0.5	4.2
P2S3	32	78	85	90	124	22.2 ± 1.0	085.0 ± 03.6	42.3 ± 2.5	1.64 ± 0.3	3.5
P3S1	30	76	81	85	123	23.5 ± 0.5	102.0 ± 15.7	34.3 ± 4.0	1.00 ± 0.2	2.1
P3S2	34	79	85	90	124	19.5 ± 1.1	076.0 ± 04.4	36.3 ± 4.0	0.76 ± 0.5	1.6
P3S3	40	79	85	90	124	14.6 ± 0.5	057.3 ± 04.5	36.3 ± 3.1	0.55 ± 0.2	1.2
P4S1	34	78	83	87	123	20.0 ± 0.1	066.0 ± 07.9	35.0 ± 2.0	0.81 ± 0.8	1.7
P5S1	42	79	87	92	124	17.1 ± 0.4	050.3 ± 03.5	38.3 ± 1.5	0.51 ± 0.7	1.1
P1S1T1	67	97	103	110	124	14.0 ± 0.3	009.3 ± 02.5	43.4 ± 2.1	0.07 ± 0.0	0.2

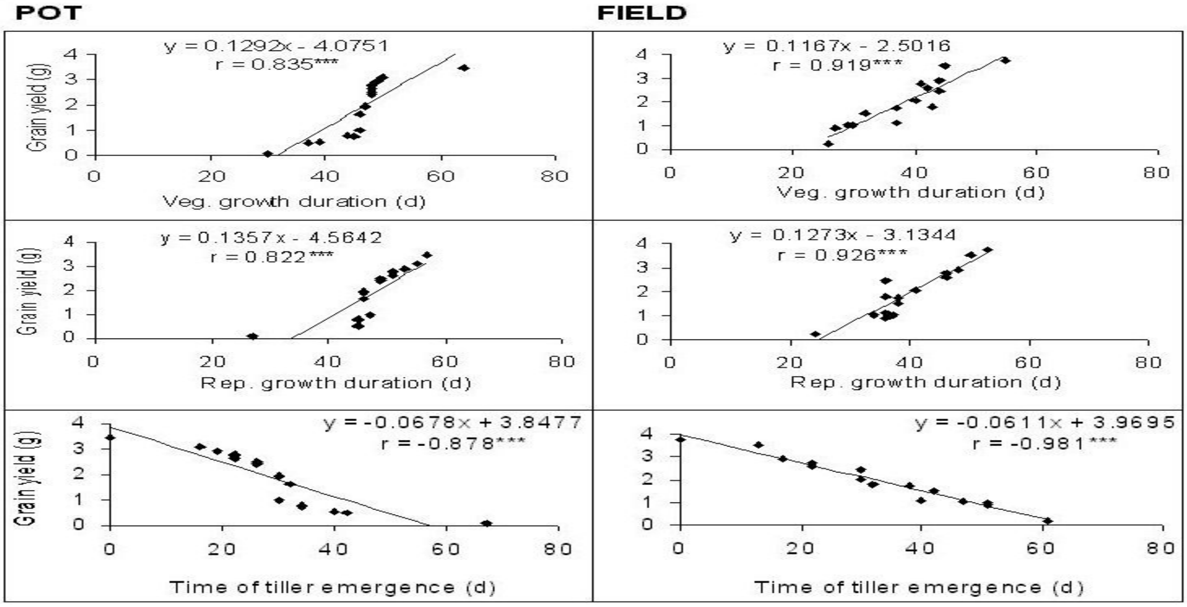

Fig 5. Relationships between vegetative growth duration (top), reproductive growth duration (middle), time of tiller emergence (bottom) and grain yield at maturity of different type of tillers of high yielding rice cultivar Lalat under pot (left) and in the field (right) conditions.

endosperm at maturity were considered sterile (Gunawardena et al., 2003). The time of anthesis was recorded when protrusion of the first dehiscing anthers in the terminal spikelets (De Datta, 1981) occurred in at least 50% plants.

Biochemical Analyses

The dried plant parts were dipped into boiling 80% aqueous methanol for 15 min in a hot water bath and the extract was transferred to a volumetric flask. The residue was boiled for a second time in 50% aqueous methanol and both the extracts were pooled together. The size of the flask varied with the size of the sample. The volumetric flask was made up to the mark with distilled water. Aliquots of the extract were taken for the estimation of soluble carbohydrates (Buysee and Merck, 1993). The residue after methanolic extraction was digested with 3% HCl for 3 hours and diluted with distilled water before it was used for the estimation of starch (Buysee and Merck, 1993). The loss of assimilates in respiration during drying was negligible. This inference could be reached after comparing sugar concentrations of the fresh and dry plant materials in trial samples.

Results

Morphological and phenological attributes

In pot condition, the primary tillers of the first five nodes of the mother shoot (P1 to P5), secondary tillers on the first three nodes of primary tillers P1, P2 and P3 (P1S1 to P1S3, P2S1 to P2S3, and P3S1 to P3S3), and first node of P4 (P4S1) and P5 (P5S1) were found to be productive (Table1). The grain yield and percentage of yield contribution of the tillers declined in an acropetal fashion from the main shoot to the last productive tiller in both the conditions; the order of decline was less related to spatial than temporal spacing of the tillers. In the field condition the rate of decline for grain yield ($y = -0.2102x + 3.6304$) and percentage of yield contribution ($y = -0.7232x + 12.486$) were steeper than the pot condition (grain yield $y = -0.1881x + 3.6848$; yield contribution $y = -0.3995x + 7.834$). The total grain weight of the plant was significantly higher in the pot condition than that in the field, as tiller number decreased in the latter (Table 2). In contrast to the pot situation, productivity was limited to the first four primary tillers (P1 to P4), three secondary tillers of the first two primary

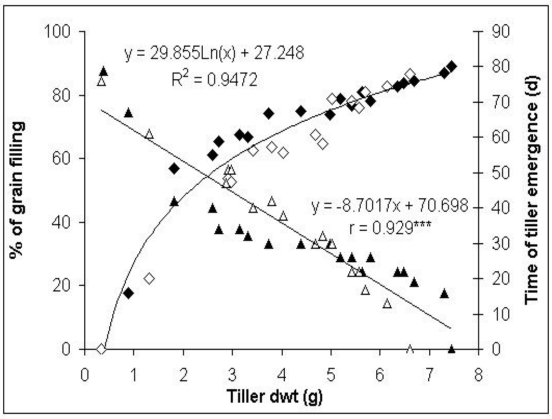

Fig 6. Relationship between tiller dry weight and percentage of grain filling (rectangles) and time of tiller emergence and tiller dry weight (triangles) in different types of tillers of rice cultivar Lalat under pot (closed symbols) and in the field (open symbols) conditions.

tillers (P1S1 to P1S3 and P2S1 to P2S3) and two secondary tillers of the third primary tiller (P3S1 and P3S2) and one secondary tiller of the fourth primary tiller (P4S1). The percentage of yield contribution of many of these tillers of the field condition was higher than their counterpart in the pot condition and grain yield of the main-shoot and primary tillers of the former condition were either higher or equal to that of the latter. The total grain yield, number of fertile grains, length, average grain weight and grain yield contribution of the panicle of the mother tiller was maximum and it decreased acropetally among the tillers belonging to both primary and secondary categories. Similar pattern of decreases was observed in the duration of vegetative and reproductive growth phases and grain filling period of both the types of tillers. However, the asynchrony in duration of development between tillers was much lower in the primary tillers in comparison to the secondary. There was very little variation in the date of maturity of the tillers and all the tillers reached the stage within a period of three days.

Tiller height and leaf area

The shoot of the tiller in both field and pot conditions grew steadily in length with passage of time and became stable a few weeks before maturity. The primary tillers extended rapidly and reached the height similar to that of the mother tiller at the maturity stage. Extension growth of the shoot was also rapid in the secondary tillers, but not as fast as that of the primary tillers. The unproductive tertiary tillers extended very slowly and possessed the minimum height at the time of maturity (data not shown). Similar hierarchy was noticed in the leaf area among different categories of tillers (data not shown). Leaf area of the first three types of tillers increased up to 10 and 8 weeks after the first tiller emergence in the pot and field conditions respectively and declined thereafter till maturity. Leaf area of different categories of tillers was higher in the pot condition than that of the field condition. Average leaf area of a primary tiller was nearly identical to that of the main shoot; but it was significantly lower in the secondary tiller. The tertiary tillers emerged very late and had the smallest duration of leaf area extension.

Panicle and shoot dry mass

Hierarchical pattern of dry mass accumulation in the shoot (above ground biomass excluding panicles) and panicle was observed among the tillers during the grain filling period in both pot and field conditions; the rate of growth was faster in the former than the latter (Fig. 1). Dry mass accumulation was highest in the mother shoot and it decreased acropetally among different types of tillers in a succession. The hierarchy in dry mass distribution was more evident among the tillers of the field condition than that of the pot condition, as slope of the regression line for decline in dry mass of tillers was sharper in the former than the latter (Fig.1).

Concentration of assimilates and starch of the panicle

The concentration of soluble carbohydrates fluctuated drastically with passage of time in the panicle of the tillers belonging to different groups in both the pot and field conditions (Fig.2). It increased sharply from booting stage to anthesis and dropped to a minimum value at maturity. The concentration of soluble carbohydrates at anthesis was highest in the panicle of the main shoot and declined acropetally among the rest of the tillers in both pot and field conditions; however, the rate of decline was faster in the field than the pot condition. In some secondary and tertiary tillers, the concentration of soluble carbohydrates of the panicle was found to be higher than the early-formed tillers at the time of maturity. In general, soluble carbohydrate concentration was higher in

Table 2. **Morphological and phenological features of the semidwarf rice cultivar Lalat grown in the field in 2004.The abbreviations are same as Table 1.** Dates of sowing and transplanting: 2.7.04 & 27.7.04. Total grain weight: 29.067±3.8g (±SD, n =3).

Type of tillers	Days from transplanting					Length of panicle (cm)	Number of grains		Weight of fertile grains (g)	% yield contribution (g)
	TE	PI	BT	AN	MA		*Fertile*	*Sterile*		
M	0	55	67	75	108	28.2 ± 0.7	157.4 ± 9.8	24.2 ± 3.2	3.75 ± 0.2	12.9
P1	13	58	68	75	108	27.9 ± 0.8	141.6 ± 6.6	29.6 ± 3.2	3.52 ± 0.2	12.1
P2	17	61	70	77	109	27.3 ± 0.9	132.2 ± 4.6	31.2 ± 2.9	2.91 ± 0.2	10.0
P3	22	63	70	77	109	26.3 ± 0.5	129.6 ± 4.7	35.6 ± 3.1	2.74 ± 0.2	09.4
P4	30	70	75	81	111	23.9 ± 0.6	081.8 ± 4.9	39.2 ± 4.2	2.03 ± 0.1	07.0
P1S1	22	64	72	78	110	26.4 ± 0.7	118.4 ± 3.8	37.4 ± 2.9	2.57 ± 0.2	08.8
P1S2	32	75	76	81	111	25.3 ± 0.8	074.2 ± 2.9	40.8 ± 3.1	1.79 ± 0.2	06.2
P1S3	40	77	79	84	113	23.8 ± 0.7	057.2 ± 1.9	34.4 ± 2.7	1.10 ± 0.1	03.8
P2S1	30	74	73	79	110	25.4 ± 0.7	109.4 ± 6.1	29.2 ± 2.6	2.44 ± 0.2	08.4
P2S2	38	75	77	83	113	24.0 ± 0.7	071.6 ± 4.4	34.2 ± 2.9	1.72 ± 0.2	05.9
P2S3	47	77	82	88	114	22.3 ± 0.7	048.2 ± 4.7	41.4 ± 3.4	1.04 ± 0.1	03.6
P3S1	42	74	75	81	112	24.1 ± 0.7	064.4 ± 3.4	36.6 ± 4.4	1.49 ± 0.2	05.1
P3S2	51	78	84	89	114	22.1 ± 0.6	043.2 ± 2.6	37.0 ± 4.0	0.91 ± 0.1	03.1
P4S1	51	80	84	89	114	21.8 ± 0.6	038.0 ± 3.5	34.2 ± 3.0	1.01 ± 0.1	03.5
P1S1T1	61	87	91	95	114	15.9 ± 0.8	011.4 ± 2.3	39.6 ± 4.0	0.21 ± 0.1	00.7

the panicle of the plants in pot condition than that of the field. The starch concentration of the panicle declined from the main shoots to the late productive tiller in a similar fashion in both field and pot conditions (Fig.2). In contrast to soluble carbohydrates, the rate of decline was faster in the pot condition than that of the field. The concentration of starch increased temporally in the panicle of all tillers from the booting stage to maturity in both the pot and field conditions; the magnitude of increase was higher in the former than the latter.

Discussion

The study identified time of emergence as the critical factor determining hierarchies in assimilate partitioning and growth dynamics between rice tillers. Ecomeristem model sensitivity analyses of rice plant suggest that supply of assimilates feeds back on demand of assimilates in growth of an organ and conversely organ production feeds back on supply (Luquet et al., 2006). In our study, the soluble carbohydrates and starch concentrations of the panicle were found to be higher in the fast growing early-tillers compared to the slow growing late-tillers. Therefore, the presence of high concentration of assimilates in the early-tillers was more due to a favourable supply from source than due to a lack of utilization in sink growth. Conversely, the concentration would have been low in the late-tillers more due to reduction in supply than consumption in growth. The soluble carbohydrates concentration of the panicle correlated positively with grain yield during the booting and anthesis stages of development and negatively at maturity in both the pot and field conditions (Fig.3). However, correlation between grain yield and starch concentration of the panicle was found to be positive through out the grain development period. Therefore, deficiency of assimilates is not a limiting factor for grain growth of the late-tillers during the later part of grain filling period. Contrast, the panicle requires more assimilates at booting or anthesis. Shortage of assimilates owing to limitation of source area during these critical stages of development might have impacted cell division and expansion in the young endosperm of the late-tillers. This evidence apparently shares the view that further increase in rice yield potential is possible through manipulation of the source rather than harvest index (Peng et al., 2000). However, panicle size of the late-tillers was smaller than the older tillers because of the short duration of growth. Consequently, limited sink capacity resulted accumulation of assimilates at maturity.

The growth conditions of the habitats strongly influenced the timings of booting and anthesis and grain yield among the tillers (Tables 1 and 2). Such variation in developmental status of tillers confers with the proposition that rice tillers produce their own flowering stimulus (Vergara and Chang, 1985). But, there was not much variation in the time of maturity among the tillers in both the habitats. The near synchronization of maturity of the tillers indicates a process of programming on the part of the plant for termination of life cycle, which might have been cued by external competition between tillers for primary resources. Poor morpho-anatomical infrastructure of late-tillers (Kim and Vergara, 1991) might have exacerbated the competition and shortened the duration of vegetative and reproductive growth (Fig. 5; Tables 1 & 2). The negative correlation between the time of tiller emergence from transplantation and soluble sugars and starch concentration of the panicle (Fig.4); and also between the same time period and grain yield in both pot and field conditions (Fig. 5) further emphasize the importance of early tillering for grain yield. A tiller enjoys photosynthetic freedom after its release from the cavity of preceding leaf sheath at emergence (William and Langer, 1975), but the time gap in achievement of independence makes it subservient in growth and development with respect to the early-tillers. Therefore, dispensing with such inferior tillers can improve synchronization of flowering and conserve resources for panicle growth of preceding tillers. In our study, low tiller number of the plant in field condition increased dominance of the early-tillers in acquiescing dry mass, grain yield and assimilates of the panicle at anthesis in comparison to the profusely-tillering plants of pot condition. Dominance of early-tillers increased, when tiller number was reduced significantly by environmental manipulations. In contrast, the late-tillers failed to use assimilates for starch synthesis as efficiently, and hence, the correlation between soluble carbohydrate concentrations at maturity and time taken for tiller emergence became positive (Fig. 4). Further, our study revealed that approximately a threshold biomass of 2.5 g per tiller is necessary for achieving at least 50% grain filling for the cultivar Lalat (Fig. 6).

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