TILLER DOMINANCE IN RICE IS DEPENDENT ON ASSIMILATE CONCENTRATION OF THE PANICLE DURING GRAIN FILLING

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SUMMARY

Considerable variation exists in grain production of rice tillers. The pattern of grain production is hierarchical; the yield of each successive tiller decreasing in an acropetal fashion from base upwards. In the present study an attempt was made to elucidate the nature of metabolic dominance of early-formed tillers in rice cultivar Jagannath during the period of grain filling by comparing the grain yield of panicle and the chemical constituents of the flag leaf and panicle of main shoot and primary and secondary tillers. Grain yield of panicle of the main shoot was maximum and the yield decreased acropetally in the tillers of the successive nodes. Growth duration of tillers also declined in the same fashion. The flag leaf of main shoot contained the highest concentration of chlorophylls, carotenoids and proteins among the tillers and the concentration was poor in the newly formed tillers. Similarly concentrations of soluble carbohydrates, free amino acids and starch of the panicle of a relatively new tiller was lower than that of an old tiller. The concentration of these chemicals remained high for a longer duration in an old tiller compared to a new tiller. It is concluded that early induction of senescence and reduction of source area might have depleted the assimilate concentration of the panicle and limited grain yield of a newer tiller than that of an older tiller.

Key words: **Assimilates, metabolic dominance, rice, tiller dynamics.**

INTRODUCTION

In semi-dwarf high yielding rice, high and early tillering capacity is considered an essential trait for optimum grain yield (Chandler 1969). The plant produces one tiller in each successive node of the culm. Usually, the late-formed tillers contribute poorly to the grain yield pool compared to those formed early (Padmaja Rao 1991). The hierarchy of tiller dominance, leading to poor yield contribution is not understood properly. Preclusion of such vital information bears heavily against development of the conceptual new plant type with 3-4 identically productive tillers (Peng *et al.* 1999). In order to develop a shy tillering variety, it is essential to understand the mechanism of assimilate partitioning between the tillers. In a low tillering cultivar, the tall culm binds more assimilates at the cost of partitioning to the late-formed tillers (Dingkuhn and Kropff 1996). In contrast, a profusely tillering variety may allow distribution of assimilates to more numbers of tillers. A tiller possesses its own independent entity after its emergence from the enclosure of the preceding leaf sheath. Assimilates and hormones produced in the tiller are largely used for its own panicle development and cross translocation to another tiller is rare (Vergara and Chang 1985, Dingkuhn and Kropff 1996). Thus, a late developed tiller may not be able to produce assimilates enough to sustain growth of the reproductive organs due to poorer photosynthetic area and older condition of the plant as a whole. In the present experiment, the objective is to identify the contribution of photosynthetic assimilates to grain yield

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of different types of tillers and thereby, understand the physiological mechanism responsible for hierarchy of tiller dominance.

MATERIALS AND METHODS

Rice (*Oryza sativa* L. cv. Jagannath) was cultivated in irrigated field condition during the wet season of 2003 in the Adaptive Research Station, Chakuli (latitude 21.29°N, longitude 84°E and altitude 178.8m). Thirty days old seedlings were used for transplantation into 10 m^2 experimental plots in three replicates. The soil of the experimental area was a sandy loam type. It was supplemented with commercial fertilizers consisting N, P_2O_5 and K_2O at 80:40:40 kg ha^{-1}. The seedlings were spaced individually at a distance of 10 x 15cm.

Plants with uniform growth and development were screened and the types of tillers developing on them were tagged. Tillers on the leaf axils of main shoot were primary tillers and tillers of primary tiller were secondary tillers. Primary tiller on the leaf axil of the first leaf (coleoptile leaf excluded) of main shoot was named P1and successive tillers were called P2, P3 etc. Secondary tiller of the first leaf axil of P1 is P1S1 and similar numbering was done for the successive tillers. The events of emergence, panicle initiation, anthesis and maturity of each tiller were recorded. The panicle and flag leaf of each type of tillers were dissected out at anthesis and subjected to chemical analyses after recording the fresh weight. The sampling continued at five days intervals up to the time of maturity. At maturity, grain number and weight, and spikelet number of the panicle were recorded.

Soluble carbohydrates and amino acids were extracted from the panicle by boiling it with 80% aqueous methanol and removing the extract into a volumetric flask. The flask was made up to the mark with distilled water. Aliquots were taken for estimation of soluble carbohydrates by addition of phenol sulphuric acid reagent (Buysee and Merck 1993) and amino acids by addition of ninhydrin reagent (Yemm and Cocking 1955). The residue was dried and ground to powder. An aliquot of the powder was digested with 3% HCl for 3 h and diluted with distilled water up to the mark in a volumetric flask. The glucose released after acid hydrolysis was measured by the phenol sulphuric acid method. The value of glucose was converted to starch by multiplying with 0.9. The flag leaf of the tillers was assayed for proteins (Lowry *et al.* 1951), photosynthetic pigments (Arnon 1949) and lipid peroxidation activity (Heath and Packer 1968).

RESULTS

Morphological attributes

There were nine productive culms including the main shoot. The primary and secondary tillers emerged in a temporal sequence; primary tiller number one (P1) emerged first and primary tiller number four (P4) was the last

Table 1. Morphological features of different types of tillers of rice cultivar Jagannath. ± values indicate standard deviations.

Types of tiller	Date of tiller emergence	Date of panicle initiation	Date of anthesis	Date of maturity	No of Grains Sterile	Fertile	Total	Grain wt. (g)	Thousand grain wt. (g)
M		3.10.03	13.10.03	17.11.03	44 ± 1.87	216.2 ± 1.48	262.2 ± 3.35	4.11±0.15	19.83±0.28
P1	19.08.03	3.10.03	13.10.03	17.11.03	56.2±1.92	181.6 ± 2.61	239.8±2.59	3.52±0.13	19.36±0.57
P2	21.08.03	3.10.03	13.10.03	17.11.03	58.24±2.05	176.31±1.75	236.21±3.54	3.52±0.09	19.36±0.50
P3	4.09.03	4.10.03	14.10.03	17.11.03	65.5 ± 3.14	168.57±3.92	230.5±4.18	3.63±0.15	19.06±0.28
P1S1	26.08.03	4.10.03	14.10.03	17.110.03	61.2 ± 2.70	172.46±3.87	232.41±4.85	3.25±0.16	18.7±0.28
P2S1	28.08.03	5.10.03	14.10.03	18.11.03	63.81 ± 3.77	161.45±4.52	225.55±2.17	2.76±0.22	18.6±0.28
P1S2	30.08.03	6.10.03	15.10.03	18.11.03	60.5 ± 4.50	150.8±3.45	210.74±5.71	2.55±0.13	18.4±0.24
P2S2	4.09.03	6.10.03	15.10.03	19.11.03	65.2 ± 3.72	128.62±4.50	194.62±4.87	2.69±0.31	18.4±0.14
P4	7.09.03	7.10.03	16.10.03	19.11.03	65.75 ± 5.2	111.78±1.95	178.43±3.22	2.71±0.26	18 ± 0.28

M = main shoot, P_1 = first, P_2 = second, P_3 = third & P_4 = fourth primary tillers.
S_1 = first secondary tiller and S_2 = second secondary tiller.

(Table 1). However, the temporal gradient in emergence of the different types of tillers was not as much visible at anthesis and maturity. The spikelet number of the main shoot was the highest among all tillers. Spikelet number decreased in an acropetal fashion among the primary tillers produced on the successive nodes of the main shoot. A similar trend in reduction of spikelet number was noticed for the secondary tillers. This trend was also evident in number of fertile grains and total grain weight of the panicle of the different categories of tillers.

Soluble assimilates and starch concentration of the panicle

The concentrations of soluble carbohydrates and amino acids of the panicle declined progressively with passage of time from anthesis to maturity stage in all the tillers (Fig.1). The reverse trend was noticed for the concentration of starch. The concentrations of these chemicals were the highest in the panicle of main shoot and lowest in the secondary tillers.

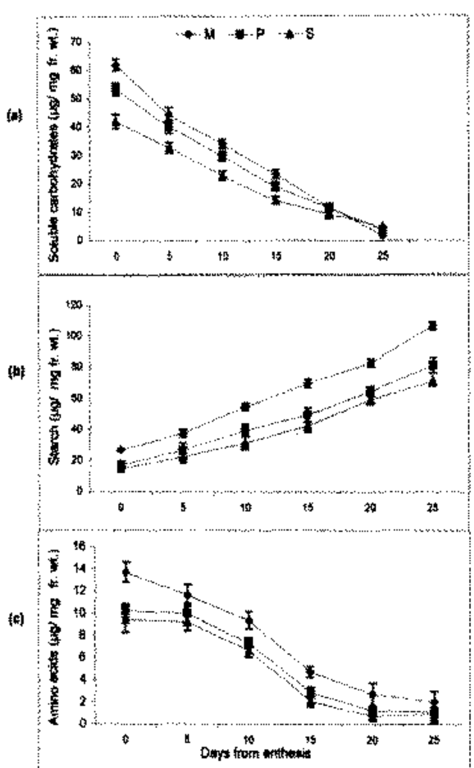

Fig. 1. Soluble carbohydrates (a), starch (b) and amino acids (c) concentrations of the panicle of different types of tillers of rice cultivar Jagannath during grain filling period. Vertical bars represent ± standard deviation values

Pigments, proteins and lipid peroxidation of flag leaf

The total chlorophyll content of the flag leaf increased temporally from anthesis before declining a few days prior to maturity (Fig.2). In contrast, the carotenoids content increased continuously with time and protein contents remained stable during the whole period of observation. These constituents were present in maximum concentration in the flag leaf of main shoot and minimum in that of the secondary tiller. Lipid peroxidation was the highest in the flag leaf of main shoot and the lowest in that of the secondary tiller, but the differences between the tillers were not significant on many occasions.

DISCUSSION

Williams and Langer (1975) and Williams *et al.* (1975) studied the tillering pattern of wheat plant and proposed that a combination of physical constraints inside leaf sheath, hormones and nutrients determine the emergence and growth of tillers. In the present study, the importance of nutrients, especially the photosynthetic assimilates, in tiller growth has been emphasized. It is apparent that a positive correlation exists between panicle growth and assimilate concentration of the tillers. Poor growth, low grain yield and high sterility of the panicle of new tillers may be due to deficiency of assimilates at anthesis and later stages of grain development. There are examples, where poor supply of assimilates to the panicle is reported to cause grain loss and spikelet failure in rice (Wang 1981, Murty and Murty 1982). Deficiency of assimilates is also proposed as the reason behind poor filling of grains in heavy-panicled rice (Khush and Peng 1996). It is also reported that the late-formed tillers become less productive owing to poor supply of assimilates (Padmaja Rao 1991). In contrast, strong metabolic dominance in the synthesis of starch noticed in the panicle of the main shoot may be due to presence of high concentration of the assimilates inside it. Provision of high concentration of assimilates in the growing panicle might have improved grain yield and spikelet number of the early formed dominant tillers. The importance of assimilates in the regulation of panicle growth has also been high lighted by several rice researchers (Murata and Matsushima 1975, Yoshida 1981).

In the present study, photosynthetic activity of the old tillers was maintained for a longer duration compared

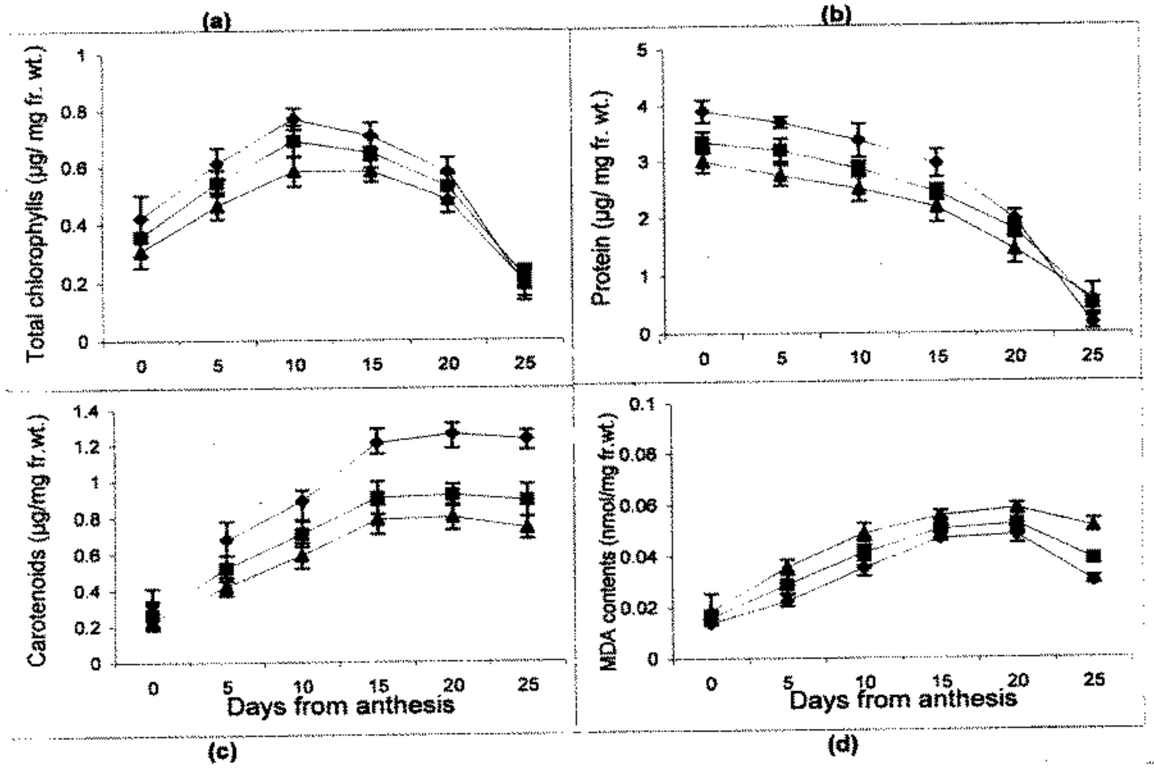

Fig. 2. Total chlorophylls (a), protein (b), carotenoids (c) and malondialdehyde (d) concentrations of the flag leaves of different types of tillers of rice cultivar Jagannath during grain filling period. Vertical bars represent ± standard deviation values. The symbols are same as Fig. 1.

to the new tillers. Senescence of the source leaf (flag leaf), as evident in breakdown of photosynthetic pigments and proteins (Fig. 2), was faster in the newly formed tillers than that of older tillers. Faster degradation of leaf structure and lower concentration of photosynthetic pigments and proteins might have deprived the new tillers adequate provision of assimilates for panicle growth and grain yield. Since inter tiller transport of chemicals in rice are rare (Dingkuhn and Kropff 1996), the newly formed tillers might have been unable to use assimilates from the old tillers. Consequently, growth of the reproductive structure on the new tillers have been curtailed.

In the present experiment the time of emergence differed more than that of maturity between the tillers. Early freedom for growth ensured large photosynthetic area and metabolic dominance in panicle growth for old tillers. Consequently, a hierarchical pattern of tiller dynamics was established in the plant. We suggest that tiller number can be limited to only 3- 4 per plant, if tillering is reduced at the early stage and tiller emergence on the main shoot is synchronised. Near synchronization of maturity of the tillers with the main shoot suggests possibility of cross movement of hormonal signal between them. Thus, an empirical approach in molecular biology may not be unsuccessful in manipulating the hormones necessary for synchronization of tiller emergence and reduction of their number. The literature is silent on the hormones regulating tiller bud release of rice. But in oat (*Avena sativa* L.), kinetin stimulates tiller development, while IAA and ABA cause the reverse effect (Harrison and Kaufman 1980).

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